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## DIFFERENTIAL VIABILITY FAVORING INVERSION HETEROZYGOTES IN *DROSOPHILA WILLISTONI* [1]


A. BRITO DA CUNHA

*Departamento de Biologia Geral, Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Brasil*



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Until recently population genetics was concerned mostly with the behavior in populations of single mutant genes with easily observable effects. It is becoming more and more apparent that the organization of genes into intrachromosomal complexes, and of individual genotypes into population genotypes, are of considerable importance in the evolution of at least some Mendelian populations (Lerner; 1954). Studies on chromosomal polymorphism in natural populations of Drosophila are largely responsible for the elucidation of the internal organization of the individual and population genotypes (see Dobzhansky, 1951 and 1954 and da Cunha, 1955 for reviews). Populations of several species of Drosophila are known to be genetic systems the adaptive values of which are based on a prevalence of balanced polymorphism for blocks of genes tied together by inversions. These blocks of genes exhibit heterosis when in heterozygous condition, while the homozygotes tend to show lower adaptive values.

The mechanisms which maintain the heterosis, and hence the balanced polymorphism, are, however, relatively little known. It is evident that the adaptive superiority of a heterozygote over the homozygotes may manifest itself in a variety of ways. There may occur a differential mortality at any stage of the life cycle, favoring the heterozygotes and discriminating against the homozygotes. This may lead to disturbances of the equilibrium ratios demanded by the Hardy-Weinberg theorem. On the other hand, the heterozygotes may be more fecund, sexually more active, or ecologically more versatile than the homozygotes. This would leave the equilibrium largely undisturbed, and yet would be no less effective than differential mortality in the maintenance of heterosis. Evidence is accumulating that these various mechanisms occur not only in different species of Drosophila but even in different populations of the same species.

Dobzhansky and Levene (1948) found that, in many different natural populations of *Drosophila pseudoobscura,* the inversion heterozygotes show, on the average, higher frequencies than do the homozy-

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gotes. Epling, Mitchell and Mattoni (1953 and unpublished data) found this not to be the case in the particular populations which they have examined, although they did observe some deviations from Hardy ratios, sometimes favoring heterozygotes and at other times homozygotes. In *Drosophila robusta*, Levitan (1951a and b) found no excessive frequencies of heterozygotes, but he discovered interesting differences in the frequencies of some gene arrangements in females and in males collected in nature. In contrast to this, Philip *et al.* (1944) in *Drosophila subobscura*, and Berrie and Sansome (1948) in *Drosophila funebris*, found strong excesses of heterozygotes in at least some populations. Finally, Dobzhansky and Pavlovsky (1955) found in a population of *Drosophila tropicalis* from a certain locality in Honduras a situation approaching a balanced lethal system, with most of the wild flies being heterozygotes for a certain inversion. Other populations of the same species do not, however, show this situation at all, and may, in fact, be free of inversions. An apparently analogous situation is observed in certain populations of *Drosophila paulistorum* which inhabit the eastern slope of the Andes in Peru (unpublished data).

Although in the natural populations of *Drosophila willistoni* the greatest number of chromosomal inversions recorded in any species are found, the nature of the heterotic mechanism in this species is completely unknown, except that da Cunha (1953) found excessive frequencies of heterozygotes for some inversions in the X-chromosome. The purpose of the present article is to put on record some new evidence bearing on this problem.

Thirty strains, each derived from a single fertilized female collected at Barreiras, in the state of Bahia (see da Cunha and Dobzhansky, 1954), were used in the experiments. After these strains were kept in the laboratory in mass cultures for about a year, six experimental populations were made from them, using about equal number of flies from each strain as the foundation stock of each population. The experimental populations, nos. 5, 59, 62, 72, 80 and 257, were kept in standard population cages. The population no. 5 was fed on the yeast *Torulopsis inconspicua*, no. 59 on *Candida krusei*, no. 62 on *Rhodotorula mucilaginosa*, no. 72 on *Kloeckera apiculata*, no. 80 on *Pichia fermentans*, and no. 257 on *Pichia membranaefaciens*. The culture medium devised by Mittler (1952) has been used in all population cages. Samples on the eggs deposited in the population cages were taken after the population no. 5 ran for 17 generations from the beginning of the experiment, population no. 59 for 3 generations, population no. 62 for 17 generations, population no. 72 for 8 generations, population no. 80 for 17 generations, and population no. 257 for 6 generations. Larvae which developed from these egg samples were grown under optimal conditions, and their salivary glands were prepared by the usual method for microscopic examination.

The Barreiras population of *Drosophila willistoni* is greatly variable chromosomally; 18 different inversions have been recorded. The mean numbers of heterozygous inversions per individual in the foundation stocks of the experimental populations equalled $6.03 \pm 0.21$ per female and $4.05 \pm 0.61$ per male. Some of the inversions became more and other less frequent in the experimental populations with time; this matter will be discussed in a separate publication. Table 1 lists the observed frequencies of only six of the inversions which are of special interest, because they were present in heterozygous condition in more than half of the larvae examined. If the carriers of different gene arrangements mate at random, and if the population is at equilibrium, the only possible explanation of a frequency of heterozygotes in excess of 50 per cent is that these heterozygotes are heterotic and are favored over the homozygotes by a differential mortality. Since the experimental populations have

TABLE 1. *Heterozygotes which showed frequencies significantly greater than 50 per cent. The inversions which might not have reached equilibrium frequencies in some of the populations are marked with an asterisk (*)*

| Experiment | Number of chromosomes studied | Chromosome and inversion | Per cent heterozygous | Chi square | P |
|---|---|---|---|---|---|
| | 732 | III Hh | 61.5 | 19.278 | <.001 |
| | 732 | III Ll | 57.6 | 8.568 | .01–.001 |
| 5 | 732 | III Mm | 60.4 | 15.781 | <.001 |
| | 244 | XL Dd* | 63.9 | 9.475 | .01–.001 |
| | 244 | XL Ff* | 77.8 | 37.901 | <.001 |
| | 244 | XR Dd | 68.0 | 15.868 | <.001 |
| 59 | 512 | III Ll* | 58.2 | 6.890 | .01–.001 |
| | 912 | III Hh | 55.3 | 5.053 | .05–.02 |
| | 912 | III Ll | 59.4 | 16.219 | <.001 |
| 62 | 912 | III Mm | 60.3 | 19.377 | <.001 |
| | 400 | XL Ff | 59.0 | 6.480 | .02–.01 |
| | 400 | XR Dd | 70.0 | 32.000 | <.001 |
| | 544 | III Hh | 58.4 | 8.557 | .01–.001 |
| 72 | 272 | XL Ff* | 80.1 | 49.441 | <.001 |
| | 272 | XR Dd* | 72.0 | 26.470 | <.001 |
| | 980 | III Hh | 55.3 | 5.518 | .01–.01 |
| | 980 | III Ll | 55.5 | 5.951 | .02–.01 |
| | 980 | III Mm | 57.3 | 10.579 | .01–.001 |
| 80 | 420 | XL Dd* | 67.1 | 24.685 | <.001 |
| | 420 | XL Ff* | 67.6 | 26.076 | <.001 |
| | 420 | XR Dd | 72.4 | 42.076 | <.001 |
| | 464 | III Hh | 60.3 | 9.931 | .01–.001 |
| | 464 | III Ll | 57.7 | 5.586 | .02–.01 |
| 257 | 464 | III Mm | 57.7 | 5.586 | .02–.01 |
| | 200 | XR Dd* | 70.0 | 16.000 | <.001 |

been undergoing changes in frequencies of some of the gene arrangements, the assumption of equilibrium must be critically examined; in table 1 the inversions for which this assumption might not have been completely true in some of the populations are marked with asterisks. It may, however, be noticed that the inversions so marked in some of the populations were the same which in other populations have reached equilibrium states, and yet were present in heterozygous condition in significantly more than 50 per cent of the flies. These inversions evidently were heterotic, a differential mortality must have occurred among the larvae, even under supposedly optimal culture conditions, and this differential mortality favored the heterozygotes.

It is interesting to point out that three of the six inversions showing such heterosis are located in the X-chromosome (D and F in the left limb and D in the right limb). Since a male has a single X-chromosome, the heterosis is confined to the female sex only. This agrees with the previous observations (da Cunha, 1953) that the inversions D and XL and in XR are heterozygous in more than half of the females also in certain natural populations of *Drosophila willistoni*. What is involved here is evidently a sex-limited effect of a balanced gene combination in the X-chromosome, of a kind found by Kerr and Kerr (1952) in *Drosophila melanogaster*.

## Summary

The gene arrangements were examined in larvae from six experimental populations of *Drosophila willistoni*. Six of the eighteen inversions present in their populations were found to be heterozygous in significantly more than 50 per cent of the larvae studied. Three of the six were inversions in the X-chromosome. The heterozygotes for these inversions are evidently favored by a differential mortality in the egg or larval stage, which discriminates against the homozygotes. The existence of such heterosis for inversions in the X-chromosomes is due to a sex-limited physiological effect favoring heterozygous females.



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# TAXONOMY AND THE EVOLUTION OF GENERA, WITH SPECIAL REFERENCE TO THE FAMILY GRAMINEAE

G. LEDYARD STEBBINS

*University of California, Davis* [1]

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The problem of the origin of plant genera is discussed much less often than that of the species and speciation, and most students of plant evolution are inclined to believe that no processes are required for the origin of genera which are not operating already in the origin of species. There have, however, been some dissenters from this point of view, such as Anderson (1937), and a review of the subject from time to time seems desirable. Two questions arise in this connection: (1) to what extent are genera artificial aggregates of species, grouped together for the convenience of taxonomists, and to what extent are they natural groupings which reflect the result of evolutionary processes?, and (2) do the evolutionary principles underlying the origin of genera differ materially from those which operate in the origin of species?

One way of providing a factual basis for more reliable answers to these questions is to review examples of families in which greatly divergent opinions have existed as to the status of genera, as well as those in which generic concepts have been relatively stable. One of the most outstanding examples of the first type is the Gramineae. In this family, taxonomists have disagreed with each other on the validity of genera, and in addition cytogeneticists have in several instances found that species placed by all taxonomists in separate genera or even in different tribes show degrees of genetic relationship which in other groups are characteristic of species belonging to the same genus. I shall begin the present discussion, therefore, by analyzing some of these examples.

The first example is that of *Lolium perenne* and *Festuca elatior* (*F. pratensis*). According to most taxonomic treatments of the family Gramineae, the genera *Lolium* and *Festuca* are placed in separate tribes, the former in the Hordeae and the latter in the Festuceae. Nevertheless, hybridization between *L. perenne* and *F. elatior* has long been suspected, and has been demonstrated experimentally by Jenkin (1933), who also crossed *L. perenne* with *F. arundinacea*. Furthermore, Peto (1933) showed that the chromosomes of *L. perenne* and *F. elatior* are sufficiently homologous with each other to form a complete set of seven bivalents in their $F_1$ hybrid. Although this hybrid is almost completely sterile, Jenkin (1955f) has obtained fertile back cross derivatives from it, and by this means has shown that gene exchange between *L. perenne* and *F. elatior* is possible to a limited degree.

The question immediately arises as to whether this is truly an example of gene exchange between species remotely related to each other, or whether the conventional taxonomic positions of *L. perenne* and *F. elatior* are false indications of their actual relationships. In order to answer this question, I shall review briefly the morphological characteristics by which these two species differ from each other, as well as those which differentiate them from related species of *Lolium* and *Festuca*.

The genus *Lolium* is placed in the tribe Hordeae because its inflorescence is a

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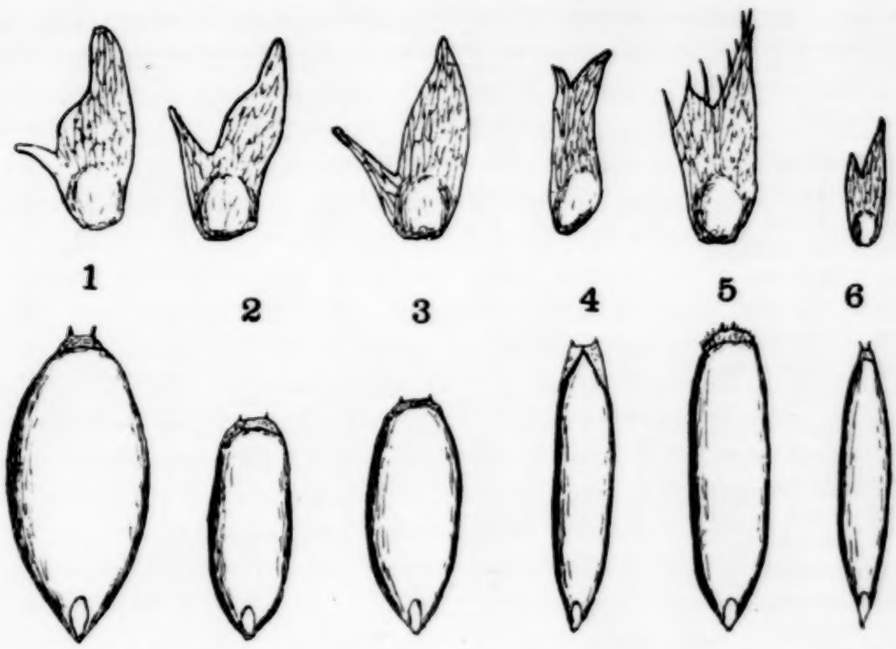
spike, rather than a panicle as in *Festuca*. This spike, however, has a completely different structure from the spike of typical Hordeae such as *Agropyron* and *Triticum*, since the spikelets are placed edgewise rather than laterally against the rachis of the spike. The only other consistent difference between the genera *Lolium* and *Festuca* is the presence of a single sterile glume in all but the terminal spikelets of *Lolium*, while *Festuca*, like nearly all other Gramineae, has two sterile glumes.

Careful study of all of the other morphological characteristics of species of *Lolium* and *Festuca* has shown that in these characteristics *L. perenne* is actually more similar to *F. elatior* than it is to other species of *Lolium*, while conversely *F. elatior* in the bulk of its morphological characteristics resembles *L. perenne* more than representative other species of *Festuca*. This fact is shown by table 1 and figures 1 to 6. The species studied were chosen as representative of various sections of their genera. *Lolium temulentum* is the best known of the weedy annual species of the genus. *Festuca idahoensis* is closely related to *F. ovina*, the type species of *Festuca*, and is essentially similar to it in the characters listed. *Festuca subuliflora* is a forest loving mesophyte of Pacific North America, perhaps related to the European *F. gigantea*, while *F. dertonensis* is an annual of the subgenus Vulpia. A glance at figures 1 to 6 shows that in respect to the perianth or lodicules, as well as the mature fruit or caryopsis, *F. elatior* is clearly more similar to *L. perenne* than to these other species of *Festuca*. The hybridization experiments of Jenkin (1933, 1955a) show that *F. elatior* is likewise closer to *L. perenne* in hybrid compatibility and fertility than to any other species of *Festuca* except for *F. arundinacea*. Furthermore, the *Festuca* species of the *ovina* complex can form occasional hybrids with *Lolium perenne* and *L. loliaceum*, and in fact are equally or more compatible with these *Lolium* species than with *Festuca elatior* (Jenkin, 1955b, c, d, e). Hence the taxonomic and cytogenetic data concerning the relationships of these species agree well with each other if taxonomic considerations are based on resemblances in respect to the majority of observable morphological characteristics, or if emphasis is placed upon the characteristics of the flower and fruit. The apparent disagreement is due to the great emphasis which, incorrectly, has been placed upon certain characteristics of the inflorescence in conventional systematic treatments of the group. In my opinion, therefore, the "genus" *Lolium* is merely a section of the large and diverse genus *Festuca*.

Other examples in the grass family of hybrids between species ordinarily placed in separate genera are particularly numerous in the tribe Hordeae. If this tribe is delimited in the stricter sense, leaving out such extraneous elements as *Lolium*, *Lepturus*, and their relatives, as well as

TABLE I. *Principal characteristics of two species of* Lolium *and four species of* Festuca

| Character | *Lolium temulentum* | *Lolium perenne* | *Festuca elatior* | *Festuca idahoensis* | *Festuca subuliflora* | *Festuca dertonensis* |
|---|---|---|---|---|---|---|
| Habitat | Field weed | Meadows | Meadows | Forest-steppe | Dense forest | Ruderal weed |
| Life span | Annual | Perennial | Perennial | Perennial | Perennial | Annual |
| Shape of leaves | Flat | Flat | Flat | Involute | Flat | Involute |
| Type of inflorescence | Spike | Spike | Panicle | Panicle | Panicle | Panicle |
| Number of glumes | One | One | Two | Two | Two | Two |
| Length lemma (mm) | 8 | 6.5 | 6 | 7 | 7.5 | 7 |
| Width lemma (mm) | 4.5 | 2.8 | 2.5 | 2.1 | 2.0 | 1.8 |
| Ratio, l/w, lemma | 1.8 | 2.3 | 2.4 | 3.3 | 3.8 | 3.9 |
| Length awn (mm) | 6–8 | 0–1 | 0–1 | 2–4 | 10–15 | 10–13 |




FIGS. 1–6. Lodicules (above, × 10) and caryopses (below, × 3) of the following species: Fig. 1, *Lolium temulentum* L., from Byron Springs, Calif., Brandegee in 1916; Fig. 2, *Lolium perenne* L., from Mt. Eddy, Calif., Heller 12125; Fig. 3, *Festuca elatior* L., from Mt. Eddy, Calif., Heller 12214; Fig. 4, *Festuca idahoensis* Elmer, from Mt. Hebron Pass, Calif., Madson in 1948; Fig. 5, *Festuca subuliflora* Scribn., from Fort Ross, Calif., Crampton 2961; Fig. 6, *Festuca dertonensis* (All.) Aschers. and Graebn., San Clemente, Calif., Beetle 3119.

*Scribneria, Jouvea,* and some other genera placed in the tribe by various systematists, it constitutes a natural grouping, well isolated from other Gramineae, except that it shows connections to *Bromus* via *Brachypodium.* It is ordinarily divided into ten genera, *Agropyron, Triticum, Aegilops, Secale, Haynaldia, Heteranthelium, Elymus, Hystrix, Sitanion,* and *Hordeum.* These genera are separated from each other almost entirely on the basis of characteristics of the inflorescence; the number of spikelets at each node of the rachis of the spike, the sessile or pedicelled character of certain spikelets, the shape of the sterile glumes, and the number of florets per spikelet.

If we disregard the little known monotypic genus *Heteranthelium,* 36 bigeneric combinations are possible between the remaining 9 genera. As is shown in table II, 20 of these combinations have either been produced artificially or are known to exist as natural hybrids. Most of these combinations are represented by several hybrids, involving different species of the parental genera, so that the total number of hybrids reported is 111. Since many species groups are infrequently cultivated, and have not been used at all in attempts at hybridization, the above number represents only a small proportion of the "intergeneric" hybrids which are possible in this group.

Such a large number of so-called "intergeneric" hybrids in one group is certainly unparallelled in the higher plants. This evidence alone indicates that the ten "genera" concerned might more properly be considered as a single genus. This point of view, moreover, is strengthened by the evidence from chromosome behavior in many of the hybrids which have been produced. The fact is now generally recognized that the best known species of the tribe, *Triticum aestivum,* contains 14 chromosomes derived from *Aegilops squarrosa* (McFadden and Sears, 1946), and recent evidence (Sarkar and Stebbins, 1956) indicates that a second set of 14

TABLE II. *"Intergeneric" hybrid combinations reported in the Gramineae, tribe Hordeae*

| Combination | $F_1$ sterile at homoploid level | $F_1$ partly fertile | Amphiploids | |
|---|---|---|---|---|
| | | | Artificial | Natural |
| *Agropyron* × *Triticum* | 10 | 0 | 3 | 0 |
| *Agropyron* × *Aegilops* | (6?) | 6(?) | 0 | 0 |
| *Agropyron* × *Secale* | 2 | 0 | 0 | 0 |
| *Agropyron* × *Haynaldia* | 1 | 0 | 0 | 0 |
| *Agropyron* × *Elymus* | 15 | 3 | 1 | 0 |
| *Agropyron* × *Hystrix* | 1 | 0 | 0 | 0 |
| *Agropyron* × *Sitanion* | 4 | 0 | 0 | 0 |
| *Agropyron* × *Hordeum* | 5 | 0 | 0 | 0 |
| *Triticum* × *Aegilops* | 32+ | 0 | 32 | 1 |
| *Triticum* × *Secale* | 2 | 0 | 2 | 0 |
| *Triticum* × *Haynaldia* | 4+ | 0 | 4 | 0 |
| *Triticum* × *Elymus* | 1* | 0 | 0 | 0 |
| *Aegilops* × *Secale* | 5 | 0 | 0 | 0 |
| *Aegilops* × *Haynaldia* | 2+ | 0 | 2 | 0 |
| *Secale* × *Haynaldia* | 1 | 1 | 0 | 0 |
| *Secale* × *Hordeum* | 1* | 0 | 0 | 0 |
| *Elymus* × *Hystrix* | 0 | 3 | 0 | 0 |
| *Elymus* × *Sitanion* | 4 | 2 | 2 | 0 |
| *Elymus* × *Hordeum* | 5 | 0 | 0 | 0 |
| *Sitanion* × *Hordeum* | 1 | 0 | 0 | 0 |
| Totals | 96 | 15 | 46 | 1 |

* Special techniques used for obtaining the hybrid.

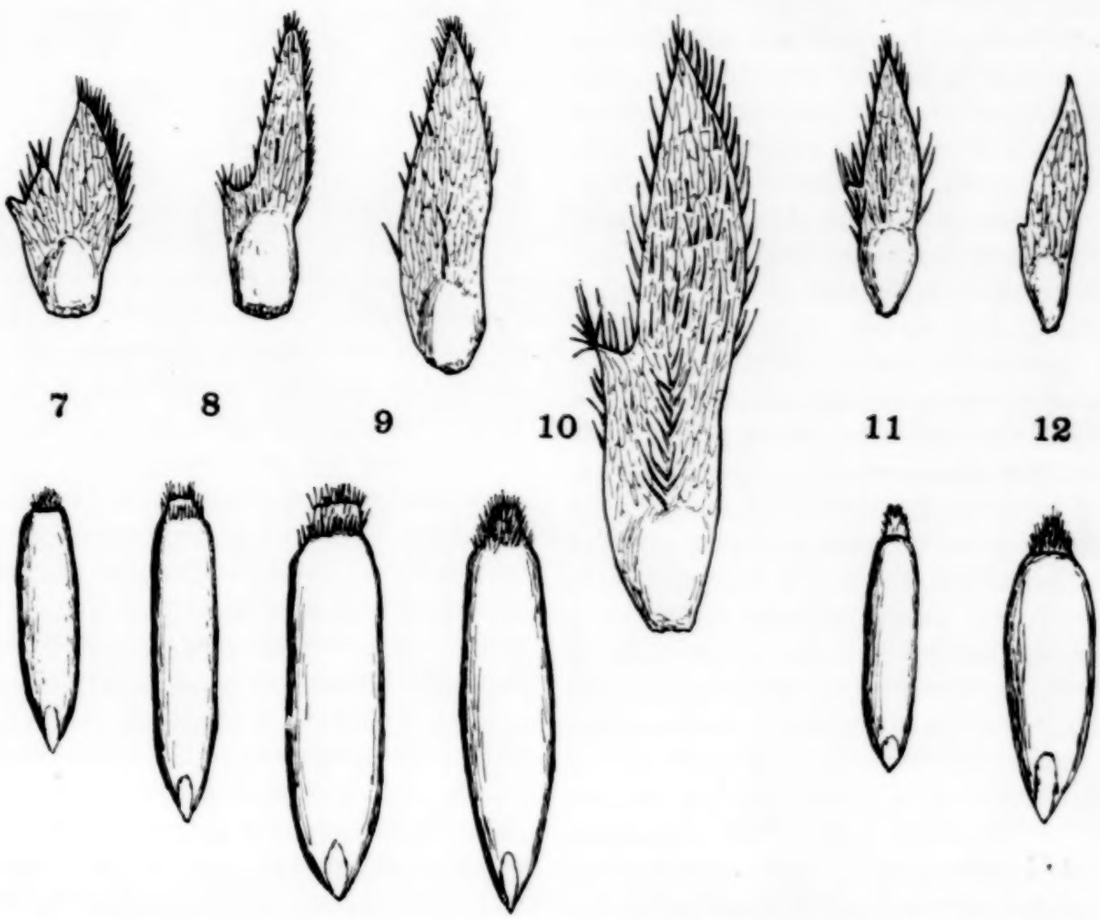
chromosomes, the "B" genome, is derived from another species of *Aegilops*. We thus reach the conclusion that the only "pure" species of *Triticum*, i.e. which does not contain chromosomes derived from *Aegilops*, is *T. monococcum* and its relatives, and the maintenance of *Triticum* and *Aegilops* as separate genera becomes an absurdity. Although the belief which has sometimes been expressed that extensive chromosome homology exists between *Triticum* and *Agropyron* is probably incorrect (Stebbins and Pun, 1953), nevertheless at least one genome of the decaploid *A. elongatum* is partly homologous with one genome of wheat.

The relationships between *Agropyron* and *Elymus* are even closer. *Elymus glaucus* has sufficient chromosome homology with *Agropyron Parishii* and *A. trachycaulum* (*"A. pauciflorum"*) so that all of the chromosomes of these three species are capable of pairing with each other (Stebbins et al 1946). Furthermore one genome in the allotetraploid *E. glaucus* is largely homologous with that of the diploid *Agropyron spicatum* (Stebbins and Singh, 1950). *Elymus glaucus* is much more closely related to these species of *Agropyron* than to some species of *Elymus*, such as *E. condensatus* and *E. triticoides* (Stebbins and Walters, 1949). The chromosome homology between *E. glaucus* and *Sitanion jubatum* is even greater (Stebbins *et al.*, 1946), and in fact on the basis of chromosome homology *E. glaucus* appears to be more closely related to *S. jubatum* than to any other species of *Elymus*. Another close connection involving species belonging to completely different sections of these genera is between *Agropyron Smithii* and *Elymus triticoides*, certain strains of which form a hybrid having complete chromosome pairing and partial fertility. These results suggest that there are many species of *Elymus* which are more closely related to *Agropyron*, *Sitanion*, and *Hystrix* than to other species of *Elymus*.

The question arises again, is this cytogenetic evidence at variance with that from external morphology, or have the

conventional generic distinctions been based upon inadequate morphological criteria? An answer to this question in respect to the four species *Agropyron Parishii, Elymus glaucus, E. condensatus,* and *E. triticoides* was given by Stebbins and Walters (1949). They compared these four species in respect to eighteen morphological characteristics plus the rhythm of flowering and the self-compatibility. They found that the four species exhibit very diverse degrees of relative similarity and difference with respect to these characters. The arrangement suggested by the generic designation, with *A. Parishii* separated from the other three species, was supported by only five of the twenty characteristics. Two other arrangements of the four species, including that suggested by the cytogenetic evidence, were also supported by five characters. In respect to the aggregate of twenty characters the four species appeared to be about equidistant from each other, and so displayed the interrelationships which one would expect to find in four species belonging to the same genus.

Additional evidence of the same nature has been obtained by examining the reproductive structures of several species of the tribe. Figures 7 to 12 illustrate the lodicules and caryopses of six representative species, *Agropyron cristatum, A. spicatum, Elymus glaucus, E. condensatus, Hordeum californicum,* and *H. glaucum.* It is evident that no differences which




FIGS. 7–12. Lodicules (above, × 10) and caryopses (below, × 3) of the following species: Fig. 7, *Agropyron cristatum* L., from Balaguer, Spain, Stebbins 5553; Fig. 8, *Agropyron spicatum* (Pursh) Scribn. and Smith, from Ravalli, Mont., Kennedy in 1925; Fig. 9, *Elymus glaucus* Buckl., from Sebastopol, Calif., Univ. Calif. Dept. Genetics 881; Fig. 10, *Elymus condensatus* Presl., from Lebec, Calif., Univ. Calif. Dept. Genetics 624; Fig. 11, *Hordeum californicum* Covas, from Ahwahnee, Calif., Crampton 1474; Fig. 12, *Hordeum glaucum* Steud. ("H. Stebbinsii Covas"), from Delhi, Calif., Crampton 1227.

would merit generic differentiation can be seen in these characters, and in fact the total amount of diversity represented by these six species in respect to lodicules and caryopses is less than that represented by the four species of *Festuca* illustrated in figures 3 to 6. Furthermore, the greatest resemblance among these species is between *Agropyron spicatum* and *Elymus glaucus,* the only two species of the six which can form a hybrid with reasonably good chromosome pairing.

Such evidence as is available, therefore, indicates that if taxonomic distinctions are based upon characters of the flowers themselves, rather than the inflorescence, and particularly if evidence from these floral characteristics is reinforced by evidence from growth habit, leaf structure, and the appearance of other parts of the plant, the evidence from external morphology can be brought into reasonably close agreement with that from cytogenetics. Both lines of evidence suggest that conventional taxonomic treatments have emphasized too much the characteristics of the inflorescence, and that the "tribe" Hordeae, sensu strictu, should be regarded as a single genus.

A further indication of the unimportance of the conventional taxonomic characters of the inflorescence as generic criteria is the discovery that the distinction which has been considered of the greatest importance in the classification of the tribe, and which has served to split it into two subtribes, may actually exist as a simple Mendelian character within a single species. *Secale cereale* is ordinarily placed in the subtribe Triticinae because its spikelets are solitary at each node of the rachis, and are oriented laterally to the rachis. We have found, however (unpublished data of H. C. Stutz), a variant in a strain of rye from Turkey in which the spikelets are regularly arranged in two's or three's at each node of the rachis, and are oriented obliquely to it, as in the subtribe Hordinae. In all other respects this variant is typical of cereal rye, and in crosses with normal plants from the same strain it behaves as a simple Mendelian recessive.

Many years ago Krause (1903) made the then very radical suggestion that the tribe Hordeae should be classified as a single genus, and proposed the generic name *Frumentum,* a proposal which runs counter to the International Rules of Nomenclature. Gould (1947) has proposed that the genera *Sitanion* and *Hystrix,* and most of *Agropyron* should be placed in *Elymus,* but specifically excludes from this genus *A. triticeum,* regarded by Hitchcock as the type species of *Agropyron.* The difficulty with Gould's proposal is its incompleteness, since no attempt is made to provide a distinction between the genera *Agropyron* and *Elymus* as he recognizes them. Hence neither of these two attempts at uniting the genera can be considered valid from the taxonomic point of view. Equally unsatisfactory are the attempts at revision of the tribe by Nevski (1934), who goes in the opposite direction, and recognizes no less than twenty genera. Some of Nevski's "genera," such as *Euagropyron, Eremopyron, Taeniatherum,* and *Aneurolepidium,* are probably valid as sections or subgenera, and his system should undoubtedly be studied and taken into account by anyone wishing to erect a new system for the tribe. Nevertheless, the recognition of his subdivisions as valid genera creates more problems of difficult generic separation than it solves, and is even more at variance with the cytogenetic evidence than is the usual treatment.

The writer believes that, although a systematic treatment of the tribe Hordeae which will express the true interrelationships of its species must begin by uniting all of the genera into one, we are nevertheless too ignorant as yet of these relationships to make a satisfactory treatment. In the groups which have been hybridized and subjected to cytogenetic study, evidence from such studies has been invaluable in suggesting relationships and in indicating which morphological differ-

ences between species and species groups have the greatest taxonomic value. Until such evidence has been obtained for all of the major subdivisions of the tribe, any taxonomic treatment which might be attempted would be subject to continuous revision. For this reason, the writer is inclined to accept for the present the conventional treatment found in the majority of contemporary floras, while recognizing that it is completely artificial.

Several other examples exist in the family Gramineae in which cytogenetic evidence has revealed the artificiality of conventional distinctions between genera. One of the best known is that of *Zea* and *Euchlaena* (Reeves and Mangelsdorf, 1942). Here, also, the two "genera" were separated on the basis of striking differences in the inflorescence. Still another example, which has yet to be worked out, is the complex of *Saccharum, Narenga, Erianthus,* and related genera, which appear to belong to a single gigantic polyploid complex. Since all of these examples have become known because they include one or more important species of crop plants, they probably represent only a fraction of the examples of this nature in the family.

On the other hand, cytological evidence has been combined with additional morphological evidence in some instances to indicate that certain traditional genera should be split. One such example is *Glyceria* and *Torreyochloa* (Church, 1949). The latter genus was first recognized as distinct from the former on the basis of differences in the number and size of its chromosomes. After this cytological difference became known, morphological differences between the genera were discovered in respect to leaf sheaths, glumes, lodicules, styles and caryopses. In another example, Hubbard (1946) has split the genus *Lepturus* into five genera. Although only a few of species concerned are known cytologically, nevertheless the morphological characters which Hubbard uses to separate his genera are for the most part similar to those which in other groups are associated with conspicuous cytological differences.

There is probably no other family of flowering plants in which cytogenetic evidence will do more to reveal the artificiality of conventional taxonomic treatments than the Gramineae. As Dr. Edgar Anderson has said (oral comm.), grasses are "streamlined," and possess a minimum of the elaborations of form which help taxonomists to make distinctions in other families. There has been a tendency, therefore, to base systematic categories upon differences in respect to one or a few conspicuous differences in the reproductive parts, particularly the inflorescence. These characters are often good indicators of relationship, but are unreliable as universal criteria, just as are characteristics of the inflorescence in other families. The morphological characteristics which reveal more consistently the true interrelationships between species and genera must therefore be sought in microscopic characters of the vegetative organs, such as the leaf epidermis and anatomy, and particularly in the structures of the flowers themselves, such as the lodicules, styles and stigmas, and caryopses. As in all groups, however, true relationships are most accurately reflected not by one or two characteristics, but by the degree of difference in respect to all observable characters, macroscopic and microscopic, vegetative and reproductive, morphological and cytological.

Although the Gramineae have been the most radically affected by taxonomic revisions based partly upon cytogenetic data, similar alterations on a smaller scale have been found necessary in other groups, as in the tribe Madiinae (Clausen, 1951) and the genus *Crepis* and its relatives (Babcock, 1947) in the Compositae, and in certain groups of the Ranunculaceae (Gregory, 1941). In every example the newer taxonomic arrangements have been based on an equal or greater number of morphological characteristics than the old ones, and the traditional arrangements have usually been shown to depend upon

differences in respect to only one or two conspicuous characters.

These examples give an effective answer to the statement which is sometimes made, namely that cytogenetic evidence can tell us much about interrelationships and evolution within genera, but is useless in explaining the origin of higher categories. In this connection it unquestionably serves at least one purpose, namely to reveal the fact that certain groups of species which all botanists have considered to belong to two or more separate genera actually are no more distantly related to each other than are other groups of species which are considered with equal unanimity to belong to a single genus.

Based upon the above discussion, I shall now attempt to answer the two questions raised at its beginning. In regard to the naturalness of recognized genera, this varies greatly from one group of angiosperms to another. Two factors apparently contribute to this variability. One is the relative abundance of diagnostic characters in some groups, and their paucity in others. In all groups like the Gramineae, in which diagnostic characters are scarce, there is a tendency to emphasize certain conspicuous, easily recognized character differences, and so to introduce a greater or lesser degree of artificiality into taxonomic treatments. In groups with an abundance of characters, like the Leguminosae and Compositae, this tendency is less marked, and the conventional taxonomic groupings are more likely to reflect the true relationships which can be verified by cytogenetic data.

The second factor contributing to variability in the interpretation and in the naturalness of genera is the presence in some groups of marked gaps between clusters of related species, and their complete absence in other groups. For instance, in the Compositae, tribe Cichorieae, the limits of some genera, such as *Malacothrix, Stephanomeria Rafinesquia,* and *Anisocoma,* are agreed upon by all taxonomists. This is because the species belonging to each one of these relatively small genera resemble each other much more in a series of characteristics than they do any species of the most nearly related genus. On the other hand, the limits of the large genera *Crepis, Lactuca,* and *Sonchus* have been defined differently by nearly every botanist who has studied them. This is because each genus contains a great diversity of types which form an intricate network or continuum of resemblances and differences in their various morphological and cytological characteristics, and some species usually placed in separate genera resemble each other as much in some characteristics as they do other species with which they are generally assumed to be congeneric. In fact, if one were to say that morphological gaps in the Cichorieae would not be valid for the separation of genera unless they were as large as that between, for instance, *Stephanomeria* and *Rafinesquia,* then one would be forced to unite *Prenanthes, Lactuca, Sonchus, Launea,* and still other genera into one huge aggregate. Differences such as this exist in every large family. They make it impossible for us to erect a system of genera in which all intergeneric gaps have the same degree of validity from the standpoint of interspecific relationships.

The examples which have been reviewed can also help us to answer the second of the two questions asked at the beginning of this discussion. If genera require any special processes for their evolution, then in a large family like the Gramineae careful study of intergeneric relationships should show the results of these processes, and one would not expect the almost unanimous opinion of taxonomists ever to be at variance with the evidence from cytogenetics. The very existence of problems like the ones discussed above indicates that the evolution of genera involves merely a continuation of the processes which cause the origin of races and species. The point at which two species groups cease to belong to the same genus and constitute separate genera must be fixed more or less arbitrarily,

since even within a single family there is no absolute yardstick for determining it.

There is, however, a change of emphasis involved in the transition from the origin of species to the evolution of genera. In the origin of species the extinction of populations plays a subordinate role, although building up barriers of reproductive isolation does cause the extinction of populations intermediate between the isolated species. In the origin of genera, on the other hand, extinction plays a much more important role. If species belonging to two or more divergent evolutionary lines exist together with their common ancestor, the latter forms a link between the representatives of the different lines, and generic separation is difficult or impossible. But with the extinction of the common ancestor and of the species which have diverged little from it, the more advanced species at the ends of the evolutionary lines will become separated from each other by increasingly wide gaps, even without further divergence on their part. For this reason, well defined genera cannot be recognized unless many species have become extinct in the family concerned.

This concept of the dominant role of species extinction in the origin of genera is supported by another line of evidence. If it were true, we should expect that the most clearly defined genera would exist in relatively old families, and particularly in those old families containing small, monotypic or ditypic genera, which are relicts. A survey of the treatment of genera in three well known manuals—Jepson's (1925) for California, Rydberg's (1922) for the Rocky Mountains, and that of Schinz and Keller (1923) for Switzerland—revealed the fact that of the numerous families containing five or more genera only five are treated exactly alike by the three authors in the delimitation of their genera. These are the Najadaceae (including Zannichelliaceae), Alismaceae, Papaveraceae, Convolvulaceae, and Lobeliaceae. The first three are relatively primitive families containing chiefly small relict genera. The last two are primarily distributed in the tropics and the southern hemisphere, so that the genera found in the north temperate zone are chiefly outliers or relicts. Furthermore, within many larger families with a primitive phylogenetic position, such as the Ranunculaceae, Saxifragaceae, and Leguminosae, the authors agree on the limits of the large majority of the genera, and differ only in their treatment of large genera which are still in an active state on evolution, such as *Ranunculus, Saxifraga,* and *Astragalus.* Widespread differences of opinion extending through whole families are found chiefly in those families with a position high on the phylogenetic scale, such as the Gramineae, Orchidaceae, Polemoniaceae, and Compositae.

The final conclusions reached from this study are therefore as follows. In relatively old families genera have become well defined through the extinction of intermediate species, and their natural limits are recognized with relative ease by taxonomists on the basis of obvious morphological characteristics. In such families cytogenetic evidence has little or no effect on the treatment obtained by the more traditional methods. On the other hand, in the more modern families, or in subdivisions of the older families which are still in an active state of evolution, species belonging to strongly divergent evolutionary lines may still be linked together by the persistence of intermediate species descended from their common ancestor. In such families, wide divergence of opinion often exists between taxonomists as to the limits of genera, and certain easily recognized morphological characters may have been overemphasized. These difficulties are especially acute in families like the Gramineae, which possess few clear cut morphological characters. In all of these more complex families taxonomic decisions should rest on studies of as many characteristics as possible, and cytogenetic evidence can be particularly helpful in pointing out the true relationships between species, so that

genera may be delimited in as natural a manner as possible. Furthermore, in such families most of the morphological characteristics which in one part of the family serve to delimit genera may in other groups have no more than specific validity, or may even vary within the confines of a single species. This situation forces us to assume that the evolution of genera is merely a continuation of those processes active in the origin of races and species, with greater emphasis on the extinction of intermediate populations.

## Summary

The morphological characteristics are reviewed of two groups of grasses in which a large number of supposed intergeneric hybrids have been obtained, namely the genera *Festuca* and *Lolium*, and the tribe Hordeae. This study leads to the conclusion that the supposed genera can be recognized only on the basis of certain conspicuous characteristics of the inflorescence, and if all of the morphological differences are considered together, or if emphasis is placed upon the perianth (lodicules) and mature fruit or caryopsis, the species concerned differ from each other no more than do different species belonging to the same genus elsewhere in the family. In other genera (*Glyceria, Lepturus*) morphological and cytological evidence indicates that these should be split. This type of evidence leads to the conclusion that the differentiation of genera comes about by means of processes which are a continuation of those operating in the origin of species, but with greater emphasis on the extinction of intermediate populations.

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# INTROGRESSION IN PLANKTONIC ROTATORIA WITH SOME POINTS OF VIEW ON ITS CAUSES AND CONCEIVABLE RESULTS

BIRGER PEJLER

*Zoological Institute, Uppsala, Sweden*

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## INTRODUCTION

During the last years introgressive hybridization has attracted notice particularly through the fundamental works of Anderson (i.a. 1949 and 1953) as a frequently active agent in the rise of new forms. For this reason it might not be without interest to demonstrate the occurrence of this phenomenon in a category of organisms which so far have hardly been mentioned in this connection, viz. the lower invertebrates, in this case the Rotatoria.

The abundant seasonal and local morphological variations within this group attracted attention relatively early. In the majority of the forms which have been the subject of more detailed investigation this morphological variation has proved more or less gradual, which has made the delimitation of species a difficult task. Polytypical species have also long been known to be of common occurrence in the taxonomy of the Rotatoria. By a detailed morphological examination and the use of statistical methods Carlin (1943) succeeded in splitting some of these old polytypical species into several new ones. Finally it must be mentioned in this connection that the characterization of the different species is usually based exclusively upon the females, since the males are usually considerably reduced and appear only during a short part of the year. In many forms (although not those treated here) they seem to be altogether missing.

## OBSERVATIONS ON *Polyarthra vulgaris* CARLIN AND *P. dolichoptera* IDELSON

The old species *Polyarthra platyptera* Ehrenberg is one of those which have been split up by Carlin. Two of the resulting species are *P. vulgaris* and *P. dolichoptera,* of which the latter had been established previously as a variety by Idelson. According to Carlin the two species (i.e., their females, see above) differ by 1) the general shape of body, 2) the position of the lateral antennae, 3) the length of the fins with regard to the body, and 4) the appearance of the fins (see fig. 1). In *P. vulgaris* the fins are relatively broad with a feebly serrated contour and "lateral nerves" in addition to a "median nerve"; the former can be observed at least distally. In *P. dolichoptera* the fins

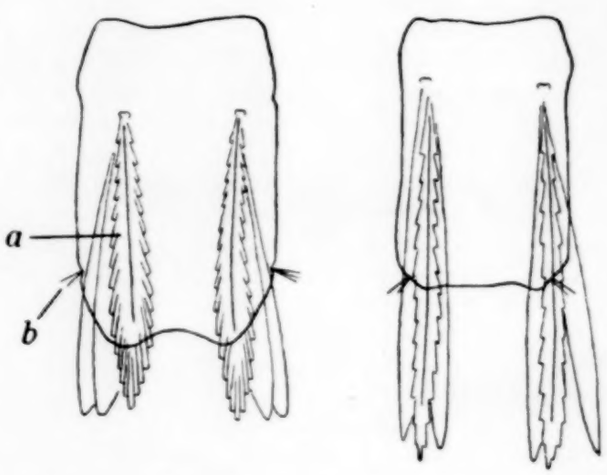


FIG. 1. *Polyarthra vulgaris* (left) and *P. dolichoptera.* Only outline of body, fins, and lateral antennae are drawn. *a* = fin, *b* = lateral antenna. Magnification 270 ×. After Carlin, 1945.

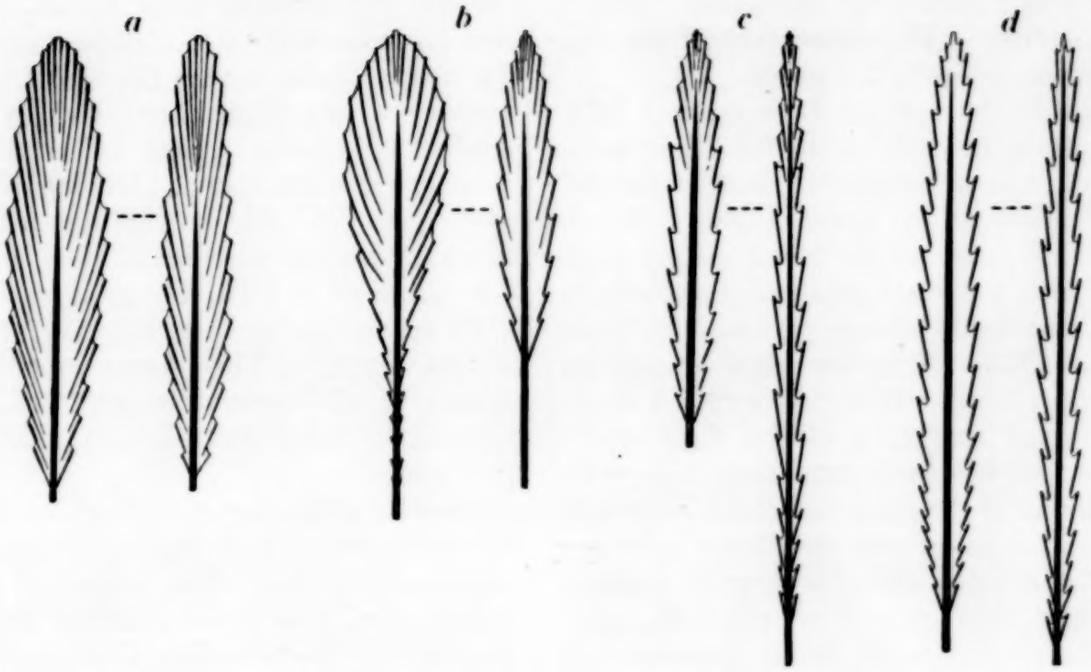


FIG. 2. Broadest and narrowest fin in four individuals of *Polyarthra*, apart from the "additional" pair of shorter fins (see Carlin, 1943). *a: P. vulgaris*, Luossajärvi, March 21, 1952. *b* and *c:* intermediate specimens, Trolltjärn (D 19), June 19, 1951. *d: P. dolichoptera*, Luossajärvi, March 21, 1952. Magnification 400 ×.

are narrower and longer with regard to the body than in *P. vulgaris;* they are also usually more strongly serrated and without "lateral nerves." In the waters examined by Carlin (particularly in Motalaström, Östergötland, Sweden) *P. vulgaris* behaves as eurythermal and *P. dolichoptera* as cold-tolerant stenothermal (oligothermal).

During the course of my examinations of the rotatorian fauna within the area of Torneträsk (NW Lapponia, Sweden), I have encountered both the mentioned species of *Polyarthra*. Of these, *P. vulgaris* is the commonest. Considering first the lakes, this species is found in all the 16 lakes at lower altitude (< 700m a.s.-l.) which have been examined, and also in two lakes at an altitude of about 1,000 meters. In the two last mentioned, the temperature never rose to + 10° C, at least not during the summer 1951. In some of the lakes at lower altitude it has not been found during the breaking up of the ice, but otherwise it occurs at all seasons and often in great abundance.

*Polyarthra dolichoptera* is much less common in the lakes of the region. It seems to be entirely absent from the waters of the high mountains. I have found it in only five of the lakes in the birch and conifer regions, and only in Luossajärvi (E 1) in great numbers. It is encountered only at temperatures below + 10° C. Its vertical distribution at the different times of sampling is represented in fig. 3, from which is also obvious that it has never been found in association with *P. vulgaris*. (My quantitative samples from the remaining lakes contain no individuals of *P. dolichoptera*.)

The *lakes* within the region have yielded no transitional forms between the species of *Polyarthra* in question. The material collected in Luossajärvi on March 21, 1952 has been treated statistically with regard to length of body and length of fins (table 1). The separation into two different populations is very clear. The group with shorter fins agrees also in the other differential characters with *P. vulgaris* as described by Carlin, while the

individuals with long fins agree with *P. dolichoptera*. The appearance of the fins is shown in figure 2 *a* and *d*.

Within the area of Torneträsk I have examined, in addition to the lakes mentioned, a large number of smaller natural accumulations of water (tarns = Swed. "tjärnar"), as a rule 1 – 3 meters deep and with a surface area roughly between 100 and 1,000 square meters. In these waters *P. vulgaris* dominates among the species of *Polyarthra*. As a rule it is absent from the tarns of the high mountains, but has been encountered in practically all of the 30 tarns which have been examined below the tree limit (situated in this area at altitudes roughly between 500 and 700 meters above sea level), particularly in samples from summer and early winter. On the other hand it is usually absent during late winter, probably in connection with the scarcity of oxygen, which then, as a rule, characterizes these smaller waters. The individuals which have been observed in summer samples agree in every respect with Carlin's description. The winter specimens often exhibit, on the contrary, characters of *P. dolichoptera*. In some cases typical specimens of *P. vulgaris* and *P. dolichoptera* have been observed together with forms transitional between the two (table 2). In other cases typical individuals of *P. vulgaris* occur together with intermediate forms, but without "pure" specimens of *P. dolichoptera* (table 3). In still other cases again only intermediate forms have been observed. As a rule the intermediate forms occupy a transitional position with regard to *all* of the properties which distinguish the two species. The appearance of the fins in two individuals of intermediate character is shown in figure 2 *b* and *c*. These illustrations show that the fins can differ from each other considerably even in one and the same individual, to a greater extent than occurs in pure individuals of *P. vulgaris* or *P. dolichoptera*. In each of the six tarns where I have observed *P. vulgaris* and *P. dolichoptera* in the same sample, intermediate forms have been found. The tarn Nissejaure (C 10) constitutes a special case. There, during the whole of the summer (June–September) and in November 1951, only typical individuals of *P. vulgaris* were found. During March and April 1952 this species appeared to be totally absent, whereas *P. dolichoptera* was observed in relatively great numbers (190 specimens in a quantitative sample of 20 litres). This latter population agreed in all essential features with the form of *P. dolichoptera* from Luossajärvi (see above).

Because of the fact that *P. vulgaris* and *P. dolichoptera* were distinguished at a comparatively late date, relatively scant information is to be found about them in literature. Nevertheless Carlin (1943) and Nipkow (1952) have subjected the two species to a detailed investigation in Central Sweden and Switzerland, respectively. Also Bartoš (1947) and Gillard (1952) report the two species from Bohemia and Belgium, respectively. Only in the work of Carlin have I found something which points to intermediate forms. He mentions, in connection with *P. dolichoptera:* "Bisweilen können die Flossen etwas breiter sein, mit weniger stark gesägtem Rande und deutlichen Seitennerven im distalen Teil der Flosse (Taf. 2, Abb. 5). Solche Individuen können eine gewisse Ähnlichkeit mit *P. vulgaris* haben, lassen sich von dieser Art aber leicht durch die Lage der Lateraltaster unterscheiden."

Concerning the ecological occurrence, it has already been mentioned that *P. vulgaris* is eurythermal, while *P. dolichoptera* occurs cold-tolerant stenothermal. This has proved to hold good for all regions which have been examined in this respect, viz. Central Sweden, (Carlin, 1943), Switzerland (Nipkow 1952), and the region of Torneträsk. In the course of my investigations it has also become apparent that *P. dolichoptera*, in contrast to *P. vulgaris*, can endure low concentrations of oxygen. Thus the amount of oxygen in Nissejaure on April 5, 1952

TABLE 1. *Relation between length of body and average length of fins in* Polyarthra vulgaris (*figures in italics*) *and* P. dolichoptera *in the lake Luossajärvi on March 21, 1952.* The specimens of *P. vulgaris* come from a depth of 2 meters, those of *P. dolichoptera* from 16 meters.

| length of body μ | length of fins 101–105 | 106–110 | 111–115 | 116–120 | 121–125 | 126–130 | 131–135 | 136–140 | 141–145 | 146–150 | 151–155 | 156–160 | 161–165 | 166–170 | 171–175 | 176–180 | 181–185 | 186–190 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 86–90 | | | | | | | | | | | | | | | | | | |
| 91–95 | | | | | | | | | | | | | | | | | | |
| 96–100 | | | | | | | | | | | | | | | | | | |
| 101–105 | | | | | | | | | | | | | | | | | | |
| 106–110 | | | | *1* | | | | | | | | | | 1 | 1 | 1 | | |
| 111–115 | | | | *1* | *1* | *3* | | | | | 1 | | | | 1 | 1 | | |
| 116–120 | | | | | *5* | *3* | | | | | | 1 | 1 | 1 | 2 | | | 2 |
| 121–125 | | | | | *2* | *4* | | | | 1 | | | 1 | | | | | |
| 126–130 | | | | | | | | | | | 1 | | | 1 | | | 1 | 1 |
| 131–135 | | | | | | | | | | | | | | | | | 1 | |
| 136–140 | | | | | | | | | | | | | | | | | | |
| 141–145 | | | | | | | | | | | | | | | | | | |
| 146–150 | | | | | | | | | | | | | | | | | | |

TABLE 2. *Variation of length of body and average length of fins in the genus* Polyarthra *in the tarn Trolltjärn (D 18) on Nov. 16, 1951.* The 40 first found specimens in a netted sample from 0–1.5 meter depth have been measured. (The tarn is at least 2 meters deep.)

| length of body μ | length of fins 101–105 | 106–110 | 111–115 | 116–120 | 121–125 | 126–130 | 131–135 | 136–140 | 141–145 | 146–150 | 151–155 | 156–160 | 161–165 | 166–170 | 171–175 | 176–180 | 181–185 | 186–190 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 86–90 | | | | | | | | | | | | | | | | | | |
| 91–95 | | 1 | | | 1 | | | | | | | | | | | | | |
| 96–100 | | 2 | 1 | | 2 | | | | | | | | | | | | | |
| 101–105 | 1 | 1 | 1 | 1 | 3 | | | | | | | | | | | | | |
| 106–110 | | 2 | | 2 | 3 | 2 | | | | | | | | | | | | |
| 111–115 | | 2 | 1 | 2 | 2 | | | | 1 | | 1 | | 1 | | | | | |
| 116–120 | | | | 2 | | | | | | | | | 1 | | | | | |
| 121–125 | | | 1 | | | | | | | | | | | | | | | |
| 126–130 | | | | | | | 1 | | | | | | | | | | | |
| 131–135 | | | | | | | | | | | | | | | | | | |
| 136–140 | | | | | | | | | | | | | | | | 1 | | |
| 141–145 | | | | | | | | | | | | | | | | 1 | | |
| 146–150 | | | | | | | | | | | | | | | | | | |

TABLE 3. *Relation between length of body and average length of fins within the population of* Polyarthra *in Trollträsk on June 19, 1951.* The 40 first noticed individuals in a netted sample, collected at the shore, have been measured.

| length of body μ | length of fins: 101–105 | 106–110 | 111–115 | 116–120 | 121–125 | 126–130 | 131–135 | 136–140 | 141–145 | 146–150 | 151–155 | 156–160 | 161–165 | 166–170 | 171–175 | 176–180 | 181–185 | 186–190 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 86–90 | | | | | | | | | | | | | | | | | | |
| 91–95 | | | 1 | | | | | | | | | | | | | | | |
| 96–100 | | | | 1 | | 1 | 2 | 3 | | 1 | | | | | | | | |
| 101–105 | 1 | 1 | | 1 | 1 | 1 | 2 | 1 | 7 | 1 | 1 | | | | | | | |
| 106–110 | | | | | | | 1 | 2 | | 2 | 1 | | | | | | | |
| 111–115 | | 1 | | | 1 | | 1 | | 1 | 1 | | | | | | | | |
| 116–120 | | | | | | | | | | 2 | | | | | | | | |
| 121–125 | | | | | | | | | | | | | | | | | | |
| 126–130 | | | | | | | | | 1 | | | | | | | | | |
| 131–135 | | | | | | | | | | | | | | | | | | |
| 136–140 | | | | | | | | | | | | | | | | | | |
| 141–145 | | | | | | | | | | | | | | | | | | |
| 146–150 | | | | | | | | | | | | | | | | | | |

was only 1.03 mg/l near the cover of ice. In Luossajärvi *P. dolichoptera* seems to dwell preferably near the bottom where the supply of oxygen is usually at a minimum (see fig. 3; on April 8, 1952 the amount of oxygen was 10.28 mg/l at 2 meters, 1.45 mg/l at 10 meters, and 0.14 mg/l at 16 meters depth). With regard to the vertical distribution of the species in Luossajärvi on June 20, 1951 it may be noted that the breaking up of the ice took place at this time with the result that the winter stratification was disturbed causing complete circulation. In the *tarns* within the region of Torneträsk *P. dolichoptera* has been encountered primarily in the neighborhood of the bottom. Yet the species does not seem to depend on a low concentration of oxygen during any phase or phases of its evolutionary cycle, since Nipkow (1952) has obtained hatching of resting eggs in water which was saturated with oxygen. The individuals developed into the first fin-less, so called *apter*a-generation, and the descendants, in the same surroundings, became typical individuals of *P. dolichoptera* with fins. For this reason their occurrence in water poor in oxygen should be interpreted in another way. It is for example conceivable that the supply of suitable food is particularly rich near the bottom. It is, furthermore, possible that *P. vulgaris* competes for the food with *P. dolichoptera* so successfully that the latter cannot live normally side by side with the former. *Polyarthra dolichoptera* would therefore be restricted mainly to surroundings poor in oxygen, which are avoided by *P. vulgaris*.

There are also obvious dissimilarities between *P. vulgaris* and *P. dolichoptera* with regard to the occurrence of the sexual periods. For *P. vulgaris* I have noted sexual periods (females carrying male eggs or resting eggs) on 28 occasions of samplings of which 10 were in lakes. All these samples, with one exception (from a tarn with intermediate forms), were taken in late summer or early winter.

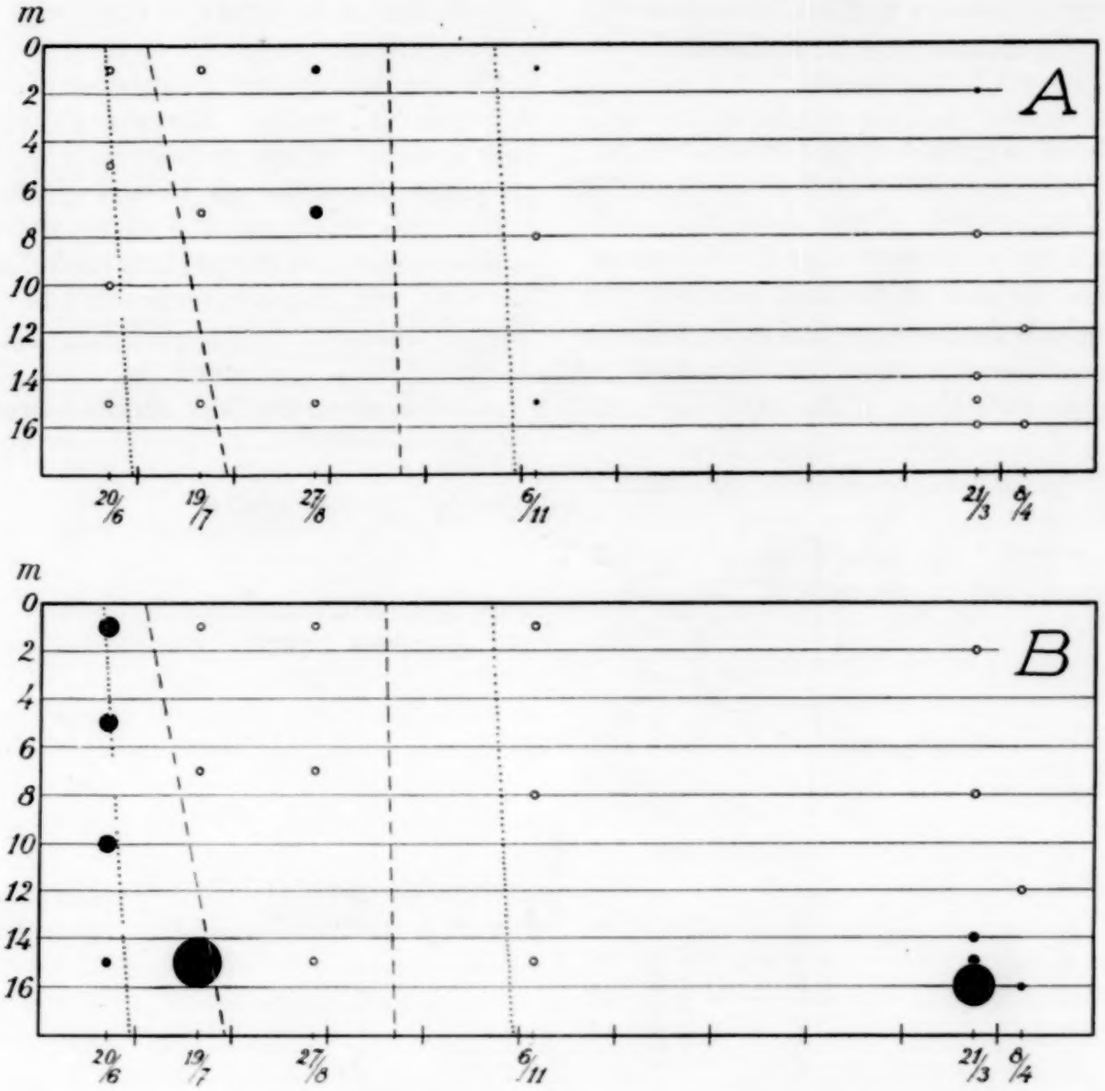


FIG. 3. Vertical distribution during different seasons (1951–1952) in the lake Luossajärvi of *Polyarthra vulgaris* (A) and *P. dolichoptera* (B). Upon the vertical axis is indicated the depth in meters (max. depth of the lake 16.5 m), upon the horizontal axis the time. Dates for the taking of the samples are indicated. Rings indicate the absence of the respective species. The area of the dots is proportional to the number of individuals upon the respective levels. The smallest dots signify a frequency of 1 specimen per liter or less, the largest (*P. dolichoptera*, July 19, 1951, depth 15 m) 100 specimens per liter. The diagram is based upon quantitative samples of 4.1 or 5 liters. Isotherms have been drawn for + 4° C (dotted line) and for + 10° C (interrupted line).

Indications of a sexual period in *P. dolichoptera* have been observed in 8 samples. Two of these samples come from lakes. In all cases but one, the samples in question have been collected immediately after the breaking up of the ice in the respective waters (middle of June). The exception refers to a tarn with abundant occurrence of intermediate forms, and here the formation of resting eggs took place in November (and in addition at the breaking up of the ice). The populations dealt with in tables 1–3 are typical in this respect: *P. vulgaris* formed resting eggs in Luossajärvi on August 27, 1951, in Trolltjärn on September 24 of the same year, *P. dolichoptera* in Luossajärvi on June 20, 1951, and June 18, 1954, in Trolltjärn (D 18) on June 19, 1951 and on June 14, 1954. In undisputable intermediate forms I have never observed the formation of resting eggs.

## Observations on *Conochilus hippocrepis* Schrank and *C. unicornis* Rousselet

In the genus *Conochilus* the females form spherical colonies of radially orientated individuals where the "feet" emanate from a common center. Glandular cells at the base of the foot secrete a mucus which forms a central jelly common to the entire colony. The appearance of a single individual of the respective species is shown in figure 4 (the jelly has been omitted).

Of the two species in question *C. hippocrepis* (*C. volvox* Ehrenberg) is the first known. When subsequently *C. unicornis* was discovered it was given its name with reference to a distinct differential character in comparison with *C. hippocrepis*, viz. the occurrence of only one lateral antenna. Nevertheless, Burckhardt (1944) has found in some lakes situated high in the Alps and in northern

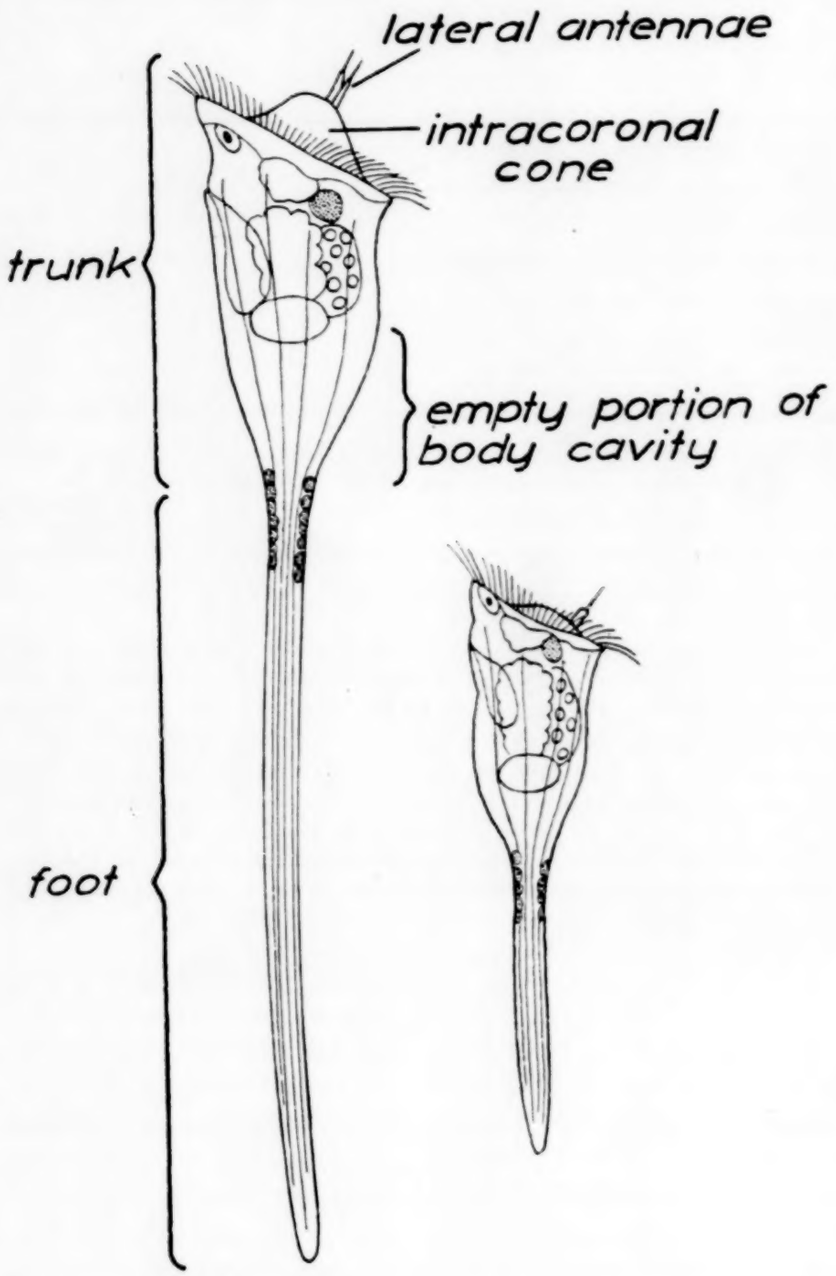


Fig. 4. *Conochilus hippocrepis* (left) and *C. unicornis*. Magnification 160 ×. After Burckhardt, 1944.

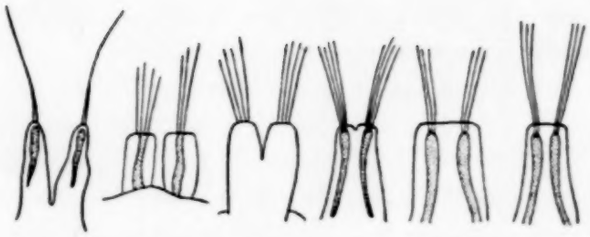

FIG. 5. Appearance of the lateral antennae (or antenna) in some individuals of *Conochilus*. The pair of antennae on the extreme left belongs to a typical specimen of *C. hippocrepis*, the antenna on the extreme right is copied from the description by Rousselet of *C. unicornis* (based upon material from England). The other antennae belong to individuals of *C. unicornis* from several Alpine lakes. After Burckhardt, 1943.

Spain, undoubted individuals of *C. unicornis* with paired lateral antennae (see figure 5). This caused Burckhardt to undertake a detailed morphological investigation of the two species, based mainly upon material from the Alps. He arrived at the result that several earlier noticed features still proved to be good distinguishing characters, but in addition he discovered a number of new ones so that, according to him, the two species are distinguished by at least 7 characters, apart from that based on the antennae, which is less reliable. The species are also said to differ in their ecological occurrence. Burckhardt's synopsis is reproduced in table 4 in a somewhat simplified form.

Only two of the waters of the region of Torneträsk have yielded specimens of *Conochilus* that agreed in all morphological points with the description of *C. hippocrepis* as given by Burckhardt. In these two waters, the lakes Vassijaure (A 20) and Rakkurijärvi (E 7), *C. unicornis* also is simultaneously present, but no indications of intermediate forms were observed. In the other localities where individuals of *Conochilus* have been observed they were either typical specimens of *C. unicornis* or intermediate forms between the two species. Intermediate forms are preponderant in general in tarns and smaller lakes. Also, in the large lake Abiskojaure (C 1), a population of intermediate character was encountered on July 26, 1954. All localities with forms of *Conochilus* are situated below the 700 meter level.

Table 5 is based upon some of the populations examined by the author. This table contains all the characters mentioned by Burckhardt with the exception of the length of the males (males have been found only in one of the samples in question). The populations form a fairly continuous series from the typical *C. hippocrepis* to forms which increasingly re-

TABLE 4. *Specific differences between* Conochilus hippocrepis *and* C. unicornis *according to Burckhardt 1944*

| Differential characters | *C. hippocrepis* | *C. unicornis* |
|---|---|---|
| 1) number of individuals in the colonies | 60–124 | usually about 15, max. 25 |
| 2) diameter of the colonies | up to 1650 μ | up to 750 μ |
| 3) length of adult females | up to 800 μ | up to 370 μ |
| 4) length of adult males | 100–110 μ | 64 μ |
| 5) ratio foot : trunk | 2.15 | 1.2 |
| 6) length of trunk : empty portion of body cavity | ≦3 | ≧5 |
| 7) the intracoronal cone | high | low |
| 8) number of lateral antennae | always 2 | usually 1, in highly situated lakes occasionally 2 |
| 9) antennae (if there are 2) parallel or diverging | diverging | almost parallel |
| 10) shape of antennae (or antenna) | distally rounded | distally flattened |
| 11) mode of life | heleoplanktonic, among aquatic plants | eulimnoplanktonic |

TABLE 5. Conochilus *spp., variation within and between some populations in the region of Torneträsk*

| | Number of individuals in the colonies | Diameter of the colonies, μ | Length of adult females, μ | Ratio foot : trunk | Length of trunk : empty portion of body cavity | The intracoronal cone | Number of lateral antennae | Antennae parallel and diverging, resp. | Shape of antennae (or antenna) | Ecology |
|---|---|---|---|---|---|---|---|---|---|---|
| Vassijaure (A 20), August 24, 1954, *a* | 30–60 | 1250 | 625 | 2.3 | ≦3 | high | 2 | diverging | not flattened distally | eulimnoplanktonic |
| Abborrsjön (A 52 small lake), August 26, 1954 | 50–55 | 1350–1470 | 560–690 | 2.0–2.5 | 3.0–3.7 | high | 1 | | not flattened distally | ? |
| Tarn C 20, July 24, 1954 | 60–65 | 1360 | 470–570 | 1.7–1.9 | 2.6–3.2 | variable | 1 | | not flattened distally | ? |
| Abiskojaure (C 1), July 29, 1954 | 25–60 | 925–1150 | 410–570 | 1.1–1.6 | 3.0–5.0 | variable | 2 | different | variable | eulimnoplanktonic |
| Tarn A 26, July 26, 1954 | 20–35 | 800–950 | 295–455 | 1.1–2.4 | 2.7–4.3 | variable | 1–2 | usually more or less diverging | variable | euplanktonic |
| C 36 (small lake), August 6, 1954 | (3–)30 | 750 | 275–335 | 1.2–1.3 | >5 | inconsiderable | 1 | | distally flattened | ? |
| Vassijaure (A 20), August 24, 1954, *b* | 10–15 | 690 | 360–365 | 1.1 | >5 | inconsiderable | 1 | | distally flattened | eulimnoplanktonic |

semble *C. unicornis*. In drawing up the table, I first arranged the different populations with regard to any one of the different characters (with the exception of the characters 2, 8, and 10). The ordinal figures obtained in this way, for every population, were added, and the arrangement in the table carried out on the basis of these sums. *Conochilus hippocrepis* and *C. unicornis*, since they were not connected by intermediate forms in Vassijaure, have been entered in the table separately (*a* and *b*, resp.) as far as this lake is concerned.

The samples entered in table 5 from the small lakes Abborsjön (A 52) and C 36 were collected near the shore. For this reason it cannot be asserted with certainty that the populations lead an euplanktonic life. It is true that the sample from tarn C 20 has been collected from the central part of the tarn with the help of a rubber boat, but as a growth of *Potamogeton* is found everywhere in this tarn I am not prepared to call the population euplanktonic in this case either.

The table shows that, with regard to the majority of the characters, the variation takes place along roughly parallel lines. To make this more evident, the ordinal figures of the different populations for the respective characters have been arranged in the form of a table (table 6).

The least amount of correlation with regard to other characters seems to be exhibited by the number of the lateral antennae.

In tarn A 26 some males were observed on July 26, 1954. These were 80–90 $\mu$ long, and thus, with respect to size, occupied an intermediate position between the males of *C. hippocrepis* and *C. unicornis* (see table 4). In connection with the population in A 26, it should be noted that no colony that contained individuals with different numbers of lateral antennae was found. This seems to indicate that this feature rests on a genetic base. The colonies in A 26 in which the individuals carried two lateral antennae were not all noticeably larger than the colonies of individuals with single antennae. No other differences were discovered.

With regard to their demands on the surroundings, I have not been able to demonstrate any differences between the two species in the region of Torneträsk. The occurrence of both is eurythermal and, at least at times, euplanktonic. In addition they are often found living side by side in the two lakes where both species have been encountered. In this con-

TABLE 6. Conochilus *spp., ordinal figures for the variables and populations contained in table 5 (the variables 2, 8, and 10 have been excluded for obvious reasons)*. The population which on comparison with the other populations exhibits the most pronounced *C. hippocrepis*-like appearance with respect to any individual variable has been given the figure 1 for this variable, etc.

| | Number of individuals in the colonies | Length of adult females | Ratio foot:trunk | Length of trunk:empty portion of body cavity | The intracoronal cone | Number of lateral antennae | Shape of antennae (or antenna) |
|---|---|---|---|---|---|---|---|
| Vassijaure (A 20), August 24, 1954, *a* | 3 | 2 | 1 | 1 | 1 | 1 | 1 |
| Abborrsjön (A 52), August 26, 1954 | 2 | 1 | 2 | 3 | 1 | 3 | 1 |
| C 20, July 24, 1954 | 1 | 3 | 3 | 2 | 2 | 3 | 1 |
| Abiskojaure (C 1), July 29, 1954 | 4 | 4 | 5 | 5 | 2 | 1 | 2 |
| A 26, July 26, 1954 | 5 | 5 | 4 | 4 | 2 | 2 | 2 |
| C 36, August 6, 1954 | 6 | 7 | 6 | 6 | 3 | 3 | 3 |
| Vassijaure (A 20), August 24, 1954, *b* | 7 | 6 | 7 | 6 | 3 | 3 | 3 |

nection it is of interest that Burckhardt (1944) characterizes *C. hippocrepis*, in contradistinction to *C. unicornis*, as heleoplanktonic (i.e. occurring only in the plankton of the tarns), and living in the macrovegetation. Also Rylov (1935) asserts that the species occurs mainly in small shallow waters, but much more rarely in lake plankton. In this latter case, Rylov thinks it highly probable that *C. unicornis* has partly been mistaken for it. (This author seems to base his conclusions mainly upon investigations in Central Europe.) In the region of Torneträsk I have, however, found typical populations of *C. hippocrepis* only in the rather large lakes Vassijaure and Rakkurijärvi, as mentioned above. Vassijaure in particular is rather deep with a maximal depth of 24 meters. This lake seems, furthermore, to be entirely without a vegetation of higher aquatic plants. The water is clear and poor in electrolytes. In a series of quantitative samples taken in Vassijaure on August 24, 1954 at the point of greatest depth the species was missing in the samples from 1, 3, and 5 meters depth, but was more or less richly represented in the samples from the other levels, viz. 10, 15, 20, and 23 meters.

Both *C. hippocrepis* and *C. unicornis* have been reported from localities in widely distant parts of the entire holarctic region, but in only two other papers (Huitfeldt-Kaas, 1906 and Lie-Pettersen, 1909) have I found unquestionable information about an eulimnoplanktonic occurrence of *C. hippocrepis*. These papers are both based upon material from Norway, and it is worthy of notice that Lie-Pettersen has also described intermediate forms between the two species of *Conochilus*, although he (like Burckhardt) has interpreted them in another way. The same conditions seem to exist in NW Ireland, since Hood (1895) supplies the following information about *C. unicornis:*

> This rare species is a lake-dweller. I found it both in 1892 and 1894 very abundant in two lakes in the Knappagh district. The large and beautiful spheres each contained from a dozen to over a hundred individuals.

Probably the number of lateral antennae has been used as the only distinctive character against *C. hippocrepis*. On the other hand the forms with double lateral antennae of *C. unicornis* observed by Burckhardt in lakes situated at high elevations in the Alps and N Spain (figure 5) agree completely with typical specimens (and colonies) of *C. unicornis*. It is, however, not inconceivable that they have been the object of a feeble introgression of *C. hippocrepis*. This is not, however, the interpretation given by Burckhardt.

I have been able to observe sexual periods in the region of Torneträsk only for *C. unicornis* and for an intermediate population (A 26). To judge, however, from the information supplied in the earlier literature (Voigt, 1904; Wesenberg-Lund, 1930; Kolisko, 1939; Burckhardt, 1944) the two species exhibit no obvious differences with regard to the season when males make their appearance.

## Discussion

The possibility that the intermediate forms mentioned might be the result of introgressive hybridization has been suggested in the preceding discussions. This is, of course, not directly obvious for it is also conceivable that the intermediate forms might represent the stock from which the extreme types arose later by differentiation. Anderson (1953, chap. 8) has discussed this possibility as opposed to the hypothesis of introgression. In connection with his own extensive material (plants) he has found five good tests that confirm the hypothesis of introgression and none that argue against it. Only the first of Anderson's tests is applicable to my material, viz. "the loose association of most of the variables into complexes demonstrable in pictorialized scatter diagrams." The truth is that I have not been able to establish diagrams of the type introduced by Anderson, but to a certain extent "the loose association" within the *Conochilus*-complex can be seen in table 6, and it appears to me traceable with regard to the intermediate forms of *Poly-*

*arthra* as well. Thus, the direct reasons for my assumption that we are dealing with introgression are not particularly powerful. Since, however, a very large number of cases among plants and some among animals, thoroughly investigated during the last years, have supported the hypothesis of introgression as opposed to the alternative hypothesis, I believe that I have good reasons for the assumption that the former is applicable in the case of my material.

If we apply Anderson's terminology (1953, p. 293) the cases reported above fall under the heading of sympatric introgression, i.e. introgression between "two species with much the same general geographical distribution separated by ecological barriers." In almost all cases of sympatric introgression established so far, the intermediate forms have been encountered in localities which had been influenced either by man or by natural catastrophies, i.e. in biotopes which had not previously existed within the regions concerned (see a.o. Anderson and Stebbins, 1954, p. 380). This does not, however, apply to my case. The biotopes of the hybrids are here relatively old; the lakes in question (e.g. Abiskojaure) must have been formed rather soon after the Ice Age. A parallel case in the same region is mentioned by Petersen (1955, p. 390). It concerns two species of butterflies, *Colias nastes* and *C. hecla*.

The appearance of sympatric introgression depends on a weakening of one or several of the factors which normally isolate two sibling species from each other (cf. Anderson 1948). Exogenous isolation can be disregarded in the case of the two pairs of species under consideration, for localities have been found for either case where the two species occur without hybridizing. It is customary to divide endogenous isolation into ecological, sexual, and genetic isolation. In my case only the ecological isolation has been accessible to analysis. It must, however, be mentioned here that amphimixis has been observed in an entirely intermediate population of *Conochilus*, the one in tarn A 26. With regard to ecological isolation, it is possible to distinguish between isolation of habitat and seasonal isolation (seasonal isolation referring to the fact that the sexual periods do not occur simultaneously in both species).

For the two species of *Polyarthra* I have established both isolation of habitat and seasonal isolation (see above). The isolation of habitat is expressed mainly as a difference in the vertical distribution within the respective waters, and is related to the increased tolerance of one of the species to a low content of oxygen. It has, however, not been possible for me to analyze the niche-creating factors, and I am unable, for this reason, to express an opinion as to whether the isolation of habitat has been weakened in localities with intermediate forms or not. On the other hand, I have been able, in isolated cases, to establish the cessation of the seasonal isolation. Nothing, however, can be said about the causes of this phenomenon. The only thing which seems at present to be established with certainty concerning the sexual periods of the Rotatoria is that they can be induced by changes in the surroundings. In spite of comprehensive investigations (a.o. by Buchner, 1941 *a* and *b*) it is still not known which factors in the surroundings are decisive in the individual cases.

Between the two species of *Conochilus* there exists isolation of habitat at least in Central Europe (inclusive of the Alps) to such an extent that *C. hippocrepis* is limited to smaller accumulations of water or to the shore of the lakes (also occurrence at the bottom in greater depths might be possible), whereas *C. unicornis* occurs as an eulimnoplanktonic form. This isolation is, however, not found within the region of the Scandinavian mountain range, or at least within large parts thereof. This fact can be interpreted either as a cause or as a result of the hybridization.

In this regard, those two lakes in the region of Torneträsk are of interest, in which these both species of Conochilus occur, in

spite of the fact that both exist in the same habitat, the plankton biotope proper. In order to survive they must occupy different niches according to Gause's principle. It appears very probable that the specialization with respect to food plays a decisive rôle (cf. Lack, 1949 and 1954) since nothing indicates the occurrence of any other niche-creating factor. According to Naumann (1923) *C. unicornis* subsists on particles smaller than about 10 $\mu$. No selection of food occurs and thus also dead seston is ingested. With regard to these facts, it appears most probable that the two species avoid competition for food by making use of particles of different size, particularly since the species of *Conochilus* differ considerably from each other in size of body. The fact that sibling species exhibit a distinct difference in size, which is reflected in the food of the respective species, is a phenomenon widely distributed throughout the animal kingdom (Lack, 1947, chap. 6 and chap. 8; Svärdson, 1954).

The more restricted the food supply is for a certain species, the lower becomes the density of individuals if other factors remain constant. This, in turn, implies an increased risk for the extinction of the species, for the reason that the meeting of males and females becomes more difficult. It is to be expected, the food in certain localities is not sufficient for two populations of *Conochilus,* while it suffices for one. By their wider variation introgressive populations should frequently have the best chances of colonizing waters poor in food. As a result of intraspecific competition such intermediate populations can also be expected to fill a larger ecological niche than either one of the two parent species, if these occur together, as the latter, by interspecific competition, push each other up towards the adaptive peaks (see Svärdson, 1949, fig. 2). According to this line of thought, one might expect to find introgressive populations of *Conochilus* mainly in localities where food is scarce. This is the case. In the majority of instances this occurs in decidedly oligotrophic, more or less humic tarns, immediately below or above the tree limit. The lake Abiskojaure (see table 5) is situated somewhat below the tree limit but contains a very poor net-plankton, probably as a result of the strong current that flows through it. Its habitus (color of the water, depth of visibility, aquatic vegetation) is suggestive of a lake in the high mountains. All of the localities with intermediate forms, as far as the planktonic Rotatoria are concerned, exhibit a decidedly lesser wealth of species than the two lakes with both species of *Conochilus.* In the former case at most 11, but usually less than 9 species are present, whereas in the latter there are 21 and 17 species, respectively. In lake Abiskojaure only 6 species have been encountered, all, with the exception of *Conochilus,* with very low frequency. An interesting parallel to my observations is mentioned by Lack (1947) in a consideration to birds of the genus *Geospiza.* Upon islands (Galapagos) where two or three species of *Geospiza* live, the species exhibit a distinct difference in size. They also have been found in general to live on foods of different size. Upon some of the smallest islands in the Galapagos archipelago, however, only a single species of *Geospiza* occurs and occasionally "occupies two food niches and has a beak of intermediate type" (op. cit., p. 85).

According to Anderson (1948), the development of introgressive forms is linked with a "hybridization of the habitat." From what has been said above about the genera *Conochilus* and *Geospiza* it seems reasonable to give consideration to a fusion of two ecological niches. According to Thienemann's is "second biocoenotic principle" (1920, p. 10) the number of species is on the whole smaller, the more extreme the living conditions. Starting from Gause's principle which was established considerably later, one might instead use the following expression: the fewer the niches the fewer the species (or better: the populations). Reduction in the number of the niches towards increas-

ingly extreme conditions should not only express itself in the elimination of niches. Occasionally fusions of niches of the kind assumed here for the species of *Conochilus* should occur, and from this point of view it appears probable that introgressive forms often have the best qualifications for colonizing biotopes which are more extreme than those of the parent species.

As has been mentioned above intermediate forms between the species of *Conochilus* have been encountered only in the Scandinavian highlands and neighboring regions, and in Ireland. It is a striking fact that a breakdown of the specific boundaries has been observed within the same regions (and also in Scotland and N Finland) for the butterfly-group of *Pieris napi* (Petersen, 1949 and 1954, fig. 6). There exists within the group of *Pieris napi*, in addition, a parallel for the sharper isolation of the species in the Alps. There *Pieris* (*napi*) *bryoniae* is split into two geographically distinct subspecies. Of these one hybridizes rather frequently, the other almost never, with *P. napi*, in spite of the fact that the distribution of the latter meets those of both subspecies (Petersen, 1955). The introgression between *Colias nastes* and *C. hecla* in the Scandinavian mountains has already been noted. As introgressive hybridization has been established within so few cases in the animal kingdom, it seems reasonable to suppose that the similar conditions with regard to the four couples of species mentioned here are not entirely fortuitous. Petersen's (1954, chap. 10) conclusions concerning holarctic sibling species are of interest in this connection. In the cases where an arctic species forms part of any of the groups of species mentioned, it seems, as a rule, to be the youngest species. With this information as a background, it should not be surprising if cases of still incomplete formation of species were encountered comparatively often in arctic regions. Such cases would be characterized by incomplete isolation of the species.

The extensive local morphological variation in planktonic Rotatoria and Cladocera has been studied by a number of scientists. Usually the variation in question has been interpreted as an adaptation to the varying conditions of the surroundings in which the mentioned organisms live. Both phenotypical and genotypical adaptation of the type caused by mutations + selection ought to occur. In my opinion the possibility of the accidental elimination of genes which takes place in small populations must not be overlooked (cf. Wright, 1948). The present investigation calls attention to hybridization as an occasionally active cause of local morphological variation. Local variation as the result of hybridization has previously been treated by several authors with regard to other organisms: concerning plants a.o. by Anderson (e.g. 1953, p. 300), concerning butterflies by Hovanitz (1949), and with respect to birds by Sibley (1954).

Anderson and Stebbins (1954) mention the possibility that species flocks might originate by introgressive hybridization. They thus think of the possibility that endemic species in ancient lakes (e.g. lake Baikal) might be the result of introgression between immigrating species. If this concept is correct, it seems to me at least equally possible that an already developed introgressive form might assert itself as an independent species when it reaches a locality with one or both of the parent species, and that by preadaptation + interspecific competition it might come to live in an ecological niche of its own. It is essential, in this interpretation, that the introgressive individuals that I have observed often live in localities where the two parent species are missing, most frequently in smaller waters with few species of Rotatoria, and thus probably also with few ecological niches (the intermediate forms of *Polyarthra* only in certain tarns, the introgressants of *Conochilus* in localities which are extremely poor in plankton, usually tarns). We can speak in terms of a low degree of isolation from the parent species. This isolation can be

maintained by the fact that introgressive individuals are capable of mating with each other, as has been observed for the intermediate population of *Conochilus* in tarn A 26.

Since introgressive hybridization has been considered only recently in taxonomic discussions it is difficult to say how wide-spread it is within the animal kingdom. It appears, however, probable that it is more common in facultatively apomiktic forms (to which most Rotatoria belong) than in most others, as Stebbins (1950, pp. 392–393) has mentioned with respect to the vegetable kingdom.

## Summary

1. Intermediate forms have been observed between *Polyarthra vulgaris* and *P. dolichoptera*, and between *Conochilus hippocrepis* and *C. unicornis*.

2. "The loose association of most of the variables" (Anderson, 1953, p. 296) within my material, but particularly comparisons with more thoroughly studied organisms (especially plants), make it probable that the intermediate forms are due to introgressive hybridization. It is a question of sympatric introgression.

3. *Polyarthra vulgaris* behaves as eurythermal, *P. dolichoptera* as cold-tolerant stenothermal. *Polyarthra dolichoptera* can, in contrast to *P. vulgaris*, live in water poor in oxygen, and occurs as a rule only in the neighborhood of the bottom. Intermediate forms have been encountered only in tarns (not in lakes). For *P. vulgaris* the sexual period occurs, as a rule, during the late summer, autumn or early winter, for *P. dolichoptera* at about the time for the breaking up of the ice. In only two cases have exceptions from this rule been observed, both in tarns with intermediate forms.

4. The two species of *Conochilus* exhibit isolation of habitat in the waters of Central Europe, but not in the two lakes within the region of Torneträsk (Lapponia, Sweden) where I have found both of them; here they both live eulimnoplanktonic, apparently without hybridizing. Introgressive forms have rarely been found together with one of the parent species (in contrast to the conditions in the species of *Polyarthra*). They have only been found in lakes or tarns with poor plankton. For this reason it appears probable that in the localities of the hybrids the supply of food is too scant to sustain more than one population of *Conochilus*. By their wider variation, introgressive forms frequently should possess the best qualifications for the colonization of these localities poor in food or, more generally, for the colonization of biotopes which are more extreme than those of the parent species.

5. A feeble isolation of the species has been observed in the Scandinavian mountain range for two couples of species of butterflies. It is possible that there exists a common cause.

6. The repeatedly mentioned local morphological variation of planktonic Rotatoria has sometimes (often ?) been caused by introgressive hybridization.

7. The introgressive forms have been found mainly in smaller waters, poor in niches, where, often, both parent species are missing. It appears probable that such forms can occasionally develop in such a direction that they come to constitute new species living side by side with their parent species if they come into new localities which are rich in niches.

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# ECOLOGIC FACTORS THAT ACCELERATE FORMATION OF RACES AND SPECIES OF TERRESTRIAL VERTEBRATES

ALDEN H. MILLER

*Museum of Vertebrate Zoology, University of California, Berkeley, California*

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In all neo-Darwinian thinking the ultimate ecologic determination of the survival of heritable changes is implicit. The ecologic forces are indeed so pervasive that we may on occasion neglect to single them out and give them full weight in the equations of functions which yield diversification and phyletic progress. We can not hope to explore on any one occasion all the intracacies of ecologic influence. Therefore, the attempt here will be to concentrate on evidence of situations and of evolutionary results that pertain to speed of diversification. More specifically, these results are (1) extensive proliferation at the racial level, and (2) quick establishment at the nascent species level of the probable roots of significant new phyletic lines or of types that will achieve faunal dominance.

Many of the functions of isolation have for long been appreciated, and the potency of small and semi-isolated breeding populations in the diversification process has been skillfully and intensively explored in recent decades, especially by Sewall Wright (1951, and antecedent papers). Certain conclusions drawn from the models based on Mendelian considerations that especially relate to the speed factor operating in ecologic settings are now well known. Random genetic drift is of course fastest in very small breeding units. But extremely small units, highly isolated, hold little chance ecologically and biogeographically of subsequent expansion unless they happen upon, in their genetic drifting, a very favorable new character or combination of characters. The small-unit effect holds much greater promise in nature by operating in species of fluctuating population levels and in a mosaic population system with partly or sporadically connected units. The speed of genetic drift will relate closely to the breeding unit size of the low points in population cycles. The quick random fixation, or approach thereto, and the subsequent proliferation of population from the altered remnant, or from any remnant, seem especially to favor rapid diversification.

Population levels in many terrestrial vertebrates undergo great changes. A recent three-year check (Genelly MS) on a marked population of California quail (*Lophortyx californica*) in a single unit of breeding area, neither deriving from nor contributing substantially to surrounding populations, showed a three-fold change in level between two successive years. There were here, in central coastal California, no drastic fluctuations in climate, merely a normal and rather slight variation in timing of annual rainfall and fog—factors that govern reproductive success. Much more spectacular of course are population fluctuations in microtine rodents, which may range from 1 to 36 per unit area, the annual minima in two successive years often showing 20-fold changes; this is due merely to die-off and repopulation at mid-latitudes, without catastrophic climatic events. These are by no means extreme examples even among vertebrates; moreover they are vastly exceeded among other organisms. Whatever may be the mechanisms of such cycles—the 3-year, 10-year, or longer types—they must be the result of some interplay with a fluctuating environment, often, it would seem of extraordinary delicacy. These fluctuations are particularly

prevalent in areas of severe and erratic climates at high latitudes and in semiarid and desert regions. These areas of great year-to-year fluctuations, through the means of drift and rebuilding from residues, if through no other, should favor quick change.

But what can drift achieve? Much as I favor the view that selection is all controlling, I can not escape the conclusion that drift will lead to exploration of untried adaptive ground. The faster and more frequent the exploration, the more chance of achieving a preadaptive workable combination that will sooner or later be seized, perfected and rapidly exploited as it enters a new adaptive level. Thus ecologically dictated cycles, and other small population effects that are partly ecological, promote elevation of gene combinations to a significant level of occurrence in the population, permitting mass trials and recombinations.

Exploratory drift in fairly rigorous isolation may also reduce the premium placed on highly compatible or mixer genes, as Mayr (1954) has well brought out. The freedom from their dominating influence may mean that new genes will be tolerated that would otherwise be lost because less miscible in the continual flow of genes through connected populations. Mixer genes are a conservative element. To be less controlled by them and thus to experiment randomly is one of the accelerations that full isolation can afford.

Moreover, insular faunas are notoriously unbalanced. Either they have never been balanced owing to difficulty of initial implant on oceanic-type islands or the faunas have become depleted owing to cyclic fluctuations in small populations that occasionally reach the vanishing point. The imbalance of course permits the well-known adaptive radiation in isolation, promoted rapidly both by the (1) opportunity of open ecologic niches and the selective advantages of filling them and being different from competitors and (2) by the nonetheless concomitant relative freedom to drift, fix, and try new combinations.

But in connection with proliferation in isolation, it is still evident that the new entities may be relatively unpromising as root stocks of new and dominant lines. To move rapidly toward new, significant species requires much trial and discard. Rigorous testing is called for and this is to be carried out in terrestrial vertebrates chiefly in large continental areas. The more testing, the quicker a distinctly new product is achieved. Exploration, by drift and selection, tends to dominate at the racial level; testing and proving dominates at the species level. The stress and trial of changing and fluctuating physical and biological environments with multiple contacts is creative.

The conclusions derived from general experience with speciation of vertebrates on continental areas of varied topographic relief is that we see in such areas not only the results of much racial proliferation that is particularly rapid but also the potentiality for quick future developments and adjustments. A mountainous area, zonated, with strong climatic contrasts, many sharp borders of plant formations, and particularly if situated near a continental edge, will provide sufficient isolation for the rapid development of races and will readily permit reinvasions, secondary junctions, introgression, fluctuating competition, and the maintenance of a reservoir of usable diversity. The tests and trials are many.

An analogy may be drawn to the structural arrangements in protoplasm which promote rapid and intricate changes. The complicated phase boundaries of the emulsion systems of protoplasm permit segregation of materials that have a maximum of surface contact with other materials. This allows quick reactions and new results. Thus complicated gene equilibria in isolated population units within reach, so to speak, of many other complicated equilibrium systems means a rapid and diversified "evolutionary metabolism."

One of the best examples of substantial

FIG. 1. Approximate breeding ranges of the 34 races of the song sparrow, *Passerella (Melospiza) melodia:* 1, *P. m. melodia;* 2, *atlantica;* 3, *euphonia;* 4, *juddi;* 5, *montana;* 6, *fallax;* 7, *saltonis;* 8, *rivularis;* 9, *goldmani;* 10, *adusta;* 11, *pectoralis;* 12, *maxima;* 13, *sanaka;* 14, *amaka;* 15, *insignis;* 16, *kenaiensis;* 17, *caurina;* 18, *rufina;* 19, *inexpectata;* 20, *merrilli;* 21, *morphna;* 22, *fisherella;* 23, *cleonensis;* 24, *gouldii;* 25, *mailliardi;* 26, *samuelis;* 27, *maxillaris;* 28, *pusillula;* 29, *heermanni;* 30, *cooperi;* 31, *micronyx;* 32, *clementae;* 33, *graminea;* 34, *coronatorum.*

racial diversification is that of the song sparrows, *Passerella* (*Melospiza*) *melodia*, of North America. The species has a continental spread and becomes much more diverse racially in the topographically and ecologically varied environments of the western border of the continent than elsewhere (fig. 1). This pattern can be repeated in lesser or greater degree over and over in terrestrial vertebrates. One cannot necessarily conclude anything about speed from such static patterns; they can be said merely to reflect the differing environmental selection pressures. But is this all? In those parts of the range of the song sparrow where isolation is fairly rigorous, races have sprung up, but elsewhere, against a background of similar ecology, they have not. The coastal marsh habitat of the Atlantic coast and of norther California are distinctive and have local differences within themselves, but they have not produced the racial multiplication seen on the shores

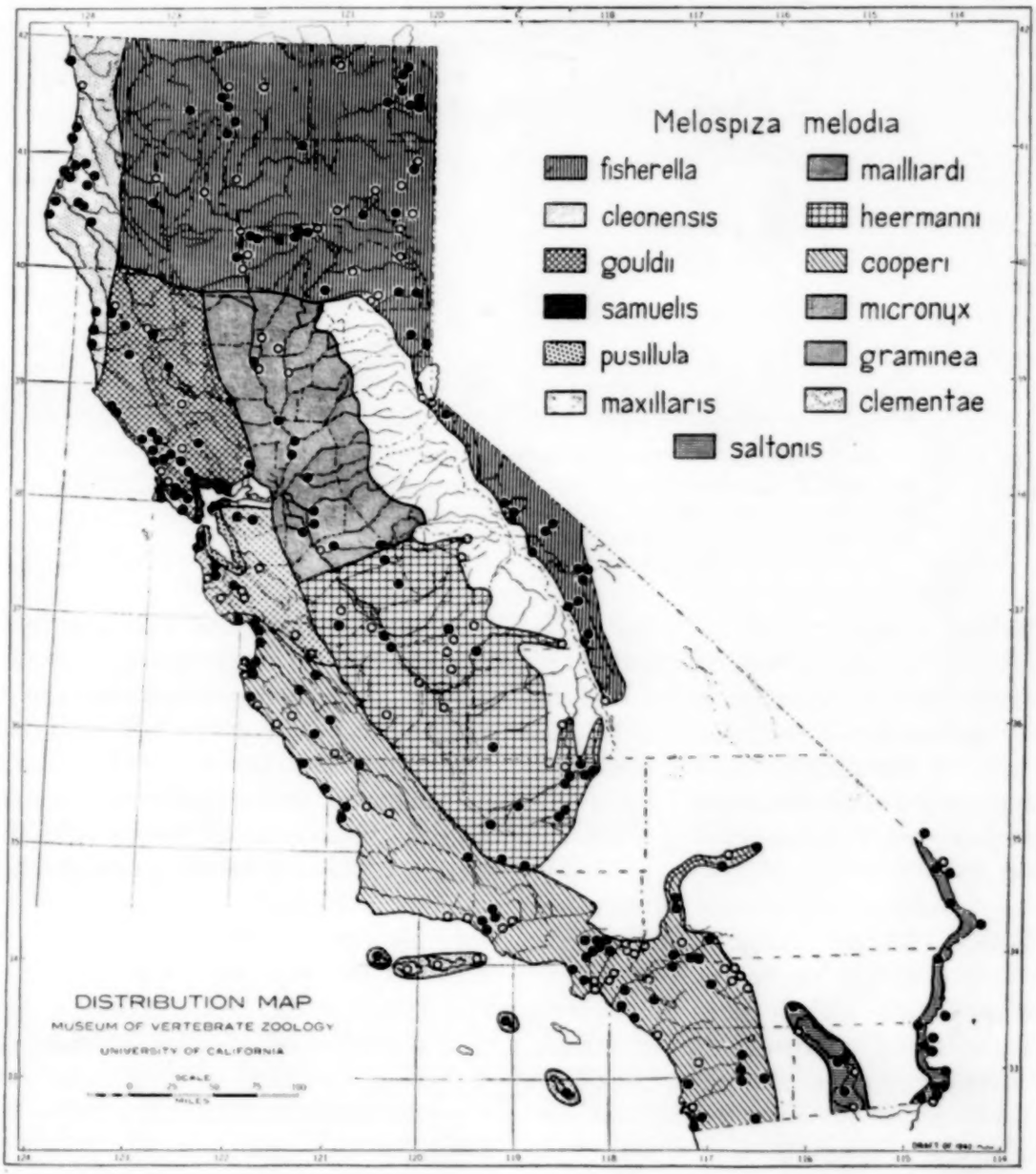


FIG. 2. Breeding ranges of races of song sparrows in California adapted from Grinnell and Miller (see Miller, 1951: 620) showing multiple differentiation in central area and on southern coastal islands.

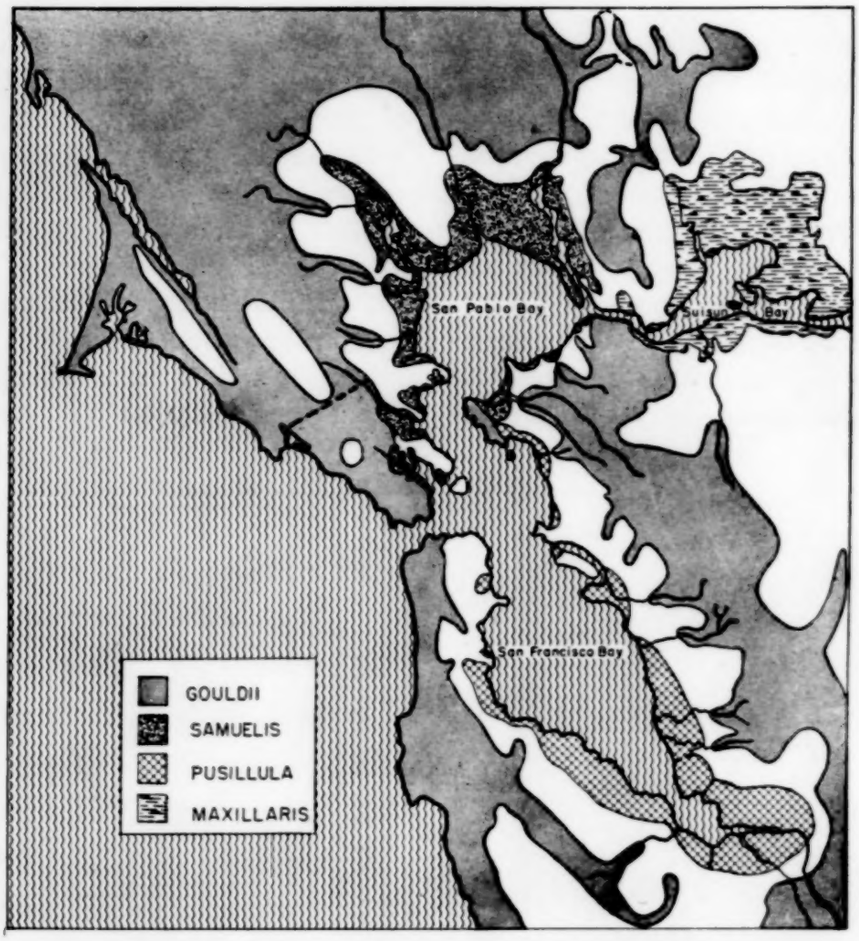


FIG. 3. Ranges of races of song sparrows in San Francisco Bay region of California showing uninhabitable areas (in white) bordering salt marsh races inland, which isolate them from upland race *gouldii*. Map adapted from Marshall (1948).

of the Gulf of Alaska and in central California (fig. 2) which have no more local ecologic diversity. Semi-isolation in these latter regions (fig. 3; Marshall, 1948) has surely sped the process during the same general period that the species has occupied other coastal areas without differentiation.

The insular *Peromyscus maniculatus* of coastal British Columbia (McCabe and Cowan, 1945) are extraordinarily diversified locally with 9 races of ordinary level and many micro-race differentiates. The diversification of these mice has been unusually great in the small insular and semi-insular situations and it has been achieved rapidly since the freedom from complete glaciation and flooding in the past 5000 to 10,000 years, and probably in a much shorter time (2000 years). It can scarcely be doubted that *Peromyscus maniculatus* has occupied western areas of comparable diversity but without such effective local isolation for 10 to 100 times as long, and probably through the whole of the Pleistocene as Blair (1953) presumes, without developing comparably numerous subspecific differentiates. Here then in the differentiation of British Columbian *Peromyscus* is speed, relative and absolute.

The nature of effective barriers to distribution operating in continental or continental-shelf insularity is of special concern, for as far as we can judge from our experience every racial differentiation among terrestrial vertebrates has been developed with the benefit of spatial sepa-

ration or allopatry of the populations concerned. It is worthwhile to mention particularly two situations which promote separation that may not be immediately obvious. These are, first, discontinuities in populations that result from borders and gaps in plant formations (especially important in birds), in soil types (especially important in small mammals and many reptiles), and in moisture sources (especially important in amphibians). Second, there is retardation or check of flow in a continuous general population as a result of inferior adaptation of individuals derived at one extreme point to the environment at the opposite extreme. This latter situation is in effect a selection barrier or filter; certainly it is imperfect, but there are signs that it is quite effective in cases of strong climatic contrasts in mountainous continental border areas. Such conditions seem to have yielded results as rapidly, to judge by multiplicity of effect, as more obvious barriers that create actual discontinuities in population.

One of the sharpest of these climatic contrasts in North America is found along the hygrogradient that runs inland from the humid northwest coast belt. We may examine the vicinity of the Humboldt-Trinity county border in California as an example. Here there is complete continuity of general habitat types; coniferous forests spread across the line and soils and stream situations are not abruptly contrasted. Yet across this line or narrow zone develops one of the greatest faunal difference scores (42; Miller, 1951) found among the relatively mobile bird groups of this region; the difference score is much higher than those (10–31) between detached conifer areas ranged in a line to the southward. Only in the comparably contrasted and detached fauna of the Great Basin mountains is the figure slightly higher (44; Miller and Russell, 1956). A score for faunal contrast is not strictly the same as an index of racial differentiation, as it is derived in part from terminations of species ranges at the line between two areas, but it is largely compiled from sets of complementary racial differentiations that occur fairly sharply at or near the line indicated. Similar changes take place in the mammalian and amphibian groups in the hygrogradient near the Humboldt-Trinity line. The desert-coastal boundaries are likewise highly effective for austral faunas.

The broad conclusion to be drawn is that ecologic contrasts on borders of continents along steep downward slopes in the hygrogradient and the cordilleran and continental shelf isolation involving either habitat or land mass or both are extraordinarily potent in racial development. Potency and speed are certainly not synonymous, but there is a reasonable assumption that they go hand in hand; at least without potency one cannot expect speed.

At the somewhat more advanced taxonomic levels of semispecies and species, introgression and hybridization are significant factors of acceleration in terrestrial vertebrates, as Anderson and G. L. Stebbins (1954) consider them to be for plants. The old argument that nothing really new can come from hybrid reshuffling seems to have been rather thoroughly allayed. To quote (pp. 378–379): "By introgressive hybridization elements of an entirely foreign genetic adaptive system can be carried over into a previously stabilized one, permitting rapid reshuffling of varying adaptations and complex modifier systems. Natural selection is presented not with one or two new alleles but with segregating blocks of genic material belonging to entirely different adaptive systems." Introgression leading rapidly to new results has been seen and documented chiefly in humanly altered environments which bring new elements into contact and create a new ,selective substrate. But also, there are many probable instances of it that have taken place before, or apart from, human influences. Introgression is particularly important as a natural operation in the "continental border—contrast topography" setting that we have been describing. Racial pro-

liferation has been achieved here. The close proximity of differentiates, at differing population densities, greatly favors numerous and quick introgressive contacts that can come from natural geologic and ecologic disturbances. Races, or their characters, may be reshuffled to arrive at favorable adaptive and compatible gene complexes and the allopatric semispecies already attained can yield species with important phylogenetic futures through testing under continental selective rigor and by borrowing improvements via introgression.

Introgressive histories of this sort are not amenable to thorough documentation after they have reached full species level. But instances of steps in the process may be noted. We may cite *Junco caniceps dorsalis,* a race so distinctly differentiated from *J. c. caniceps* to the north that some systematists would regard it as a semispecies. This form probably has been derived in considerable degree by introgression. Its black upper mandible and frequently appearing red tertial feathers are inexplicable on any basis of clinal or adaptive developments and must have been "borrowed" from a southern neighboring species in southern Arizona with which it does not now interbreed. Its size is somewhat greater than in either presumptive parent, but fundamentally this form has the main framework of characters of its northern parent, including the lack of conspicuous lipochrome pigments and of certain innate behavior patterns. Even clearer is the hybrid history of the race *Junco hyemalis cismontanus* that has been developed in northern British Columbia in postglacial time (Miller, 1941). Here a particular hybrid type seems to be gaining dominance over various other recombination types resulting from the crossing of *J. hyemalis* and *J. oreganus.* The new form favors *hyemalis* in characters and freely interbreeds with it at its borders, but it is partly isolated reproductively from *J. oreganus* and to a limited degree is sympatric with it. This instance seems to be one of those not uncommon post- or late-Pleistocene introgressive changes in plants and animals that take place in glaciated mountain areas.

Secondary junction of the kind just cited not infrequently places species status on trial. The more trials, the quicker will phyletic root stocks take hold. This kind of situation occurs particularly where short-distance dispersal in diversified terrain can easily bring about contact. In these contacts some nascent species will fail, some introgress variously, and others stand up as biologically separate in a sympatric state. Whether or not there still are residual race chains circuitously connecting the extremes is relatively unimportant, for the connections can so readily be broken by extinction. But the fact of such indirect connections provides an important element of history. Examples of species now under test or recently having been so are relatively frequent in western North America. Instances may be cited among the amphibians in *Ensatina* (R. C. Stebbins, 1949), *Batrachoseps* (Hendrickson, 1954), and *Rana* (Zweifel, 1955), in lizards in *Eumeces* (Rodgers and Fitch, 1947), in birds in *Dendrocopos* (Miller, 1951) and *Pipilo* (Davis, 1951; Sibley, 1950), and in mammals in *Peromyscus* (Blair, 1953, and others).

I have suggested that highly isolated differentiates may be thought of as unpromising or "sterile" phyletically. Their lack of trial in rigorous continental selection may be a deterrent to their establishment and spread as effective new elements in continental faunas. But actually the main reason why we see little or no evidence of such island-generated types establishing on continental areas may be the improbability of transfer. Island populations are of necessity relatively small, even if dense, and the number of dispersants is less than available in the opposite direction. Of course the target areas for such few insularly derived vagrants is relatively great, but the large size of the target itself leads to scattering of disperants and consequent failure to set up a mainland colony in the face of

competition and swamping. No easy stages in trial invasion nor repeated opportunities over short periods of geologic time are available to the island-to-mainland dispersant. Such vagrants from oceanic islands may occasionally have succeeded but probably only if they had very novel adaptive advantages. We have not found, nor are we likely to, an invasion of the mainland by Galápagos tortoises or Galápagos finches, or by Hawaiian honeycreepers.

But animals of continental shelf islands, as well as those of epicontinental ecologic islands, have apparently often dispersed or been reconnected and spread from their differentiation centers to occupy continental areas effectively. Such apparently is the history of the insularly derived species *Peromyscus polionotus* that has spread to the mainland following a period of separation in insular Florida of the Pleistocene. So likewise the white-eyed towhee, *Pipilo erythrophthalmus alleni*, of Pleistocene insular Florida has spread on the mainland, reestablishing contact at the racial level with its relatives (Dickinson, 1952) and profoundly affecting the character of the continental populations by racial introgression.

The violet-green swallow of the race *Tachycineta thalassina brachyptera* has developed as a strong and abundant differentiate of the southern half of the peninsula of Baja California. It has apparently invaded and established effectively on the opposite mainland coast of central Sonora in a limited area. So likewise has the insular race of the warbler *Vermivora celata* on the mainland peninsulas opposite the off-shore islands of southern California.

Another facet of ecologic influence with respect to speed is the effect of innate range of ecologic tolerance and explorative tendencies displayed by different species. In almost all vertebrate animals there is a strong homing instinct. Accordingly, little gene flow arises from the movements of adults. Diffusion of genetic material and pioneering comes about chiefly through the dispersal of young in the course of their establishment on home ranges or territories for purposes of their first breeding activity.

This dispersal is influenced strongly by instinctive responses to terrain and habitat and is certainly not purely a mechanical scattering on the trial and error principle. The expression habitat selection has been used for these responses. It is better described as reaction, automatic or instinctive, to certain aspects of habitat to which the species has been geared through natural selection. It does not imply selection of a habitat coincident with the limits of environmental tolerance of the species but usually reaction to some feature of habitat far within those limits which circumstance sometimes results in seemingly unnecessarily narrow restriction. There is no testing of the environment for suitability in all ways but merely an unknowing, though doubtless selectively determined, instinct to respond to key aspects of the environment that have proved safe for the species. The reactions of some species in habitat selection seem unduly conservative; other species impress us as distinctly given to pioneering.

The effect of ecologic tolerance may be estimated in part by the degree to which species have become polytypic. The obvious danger in using this criterion is that many other influences have had a part in this and we cannot prove a clear-cut, positive causal influence of environmental tolerance. Views concerning amount of tolerance may be developed to considerable degree from our detailed information about the habitat responses and natural history of the species. To minimize the effect of factors other than tolerance that contribute to the amount of polytypic differentiation, special comparisons may best be attempted between closely related species that are similar in most respects. Intrageneric comparisons are particularly called for.

We may take for example *Passerella iliaca* and *Passerella* (*Melospiza*) *lincolnii*, both annually migrant birds that

are close relatives and which occupy for breeding roughly the same areas of North America in northern latitudes and the higher life-zones. *Iliaca,* the fox sparrow, breeds in subalpine scrub, dense coastal brush of the forest border, riparian tangles, and dry montane chaparral of the southern mountains. *Lincolnii,* the Lincoln sparrow, breeds only in mountain and subarctic meadows and bogs. *Iliaca* has

FIG. 4. Approximate breeding ranges of the 18 races of the fox sparrow, *Passerella iliaca:* 1, *P. i. iliaca;* 2, *zaboria;* 3, *altivagans;* 4, *unalaschcensis;* 5, *insularis;* 6, *sinuosa;* 7, *annectens;* 8, *townsendi;* 9, *fuliginosa;* 10, *olivacea;* 11, *schistacea;* 12, *swarthi;* 13, *canescens;* 14, *fulva;* 15, *monoensis;* 16, *brevicauda;* 17, *megarhyncha;* 18, *stephensi.*

FIG. 5. Breeding ranges of the 3 races of the Lincoln sparrow, *Passerella* (*Melospiza*) *lincolnii*: 1, *P. l. lincolnii*; 2, *alticola*; 3, *gracilis*.

evolved 18 races (fig. 4) and *lincolnii* 3 races (fig. 5) in the same general area. The greater number of races in *iliaca* is not merely a multiplication of local color variations but involves some striking modifications of bill and skull of the order seen among some of the species of a single genus of the Galápagos finches. On the contrary, the races of *lincolnii* are weak color and size units. Both species show similar amounts of individual variation in single populations which suggests that variants are equally available that might lead to differentiation.

Another pair of species in the same genus provide a similar contrast. *Passerella* (*Melospiza*) *melodia* and *P. georgiana* are partly migratory and occupy middle latitudes on the continent. The races of *melodia* show extreme color differentiation and size differentiation, even more than in *iliaca*, although the bill is not modified so strikingly. *Georgiana* has evolved only weak color races. *Georgiana* does not extend to the west coast whereas *melodia* does. However, over large parts of the continent both species occur. *Melodia* has developed 34 races (fig. 1) and *georgiana* 3 races (fig. 6). *Melodia* and *georgiana* are subject to similar cli-

FIG. 6. Breeding ranges of the 3 races of the swamp sparrow, *Passerella* (*Melospiza*) *georgiana:* 1, *P. g. ericrypta;* 2, *P. g. georgiana;* 3, *P. g. nigrescens.*

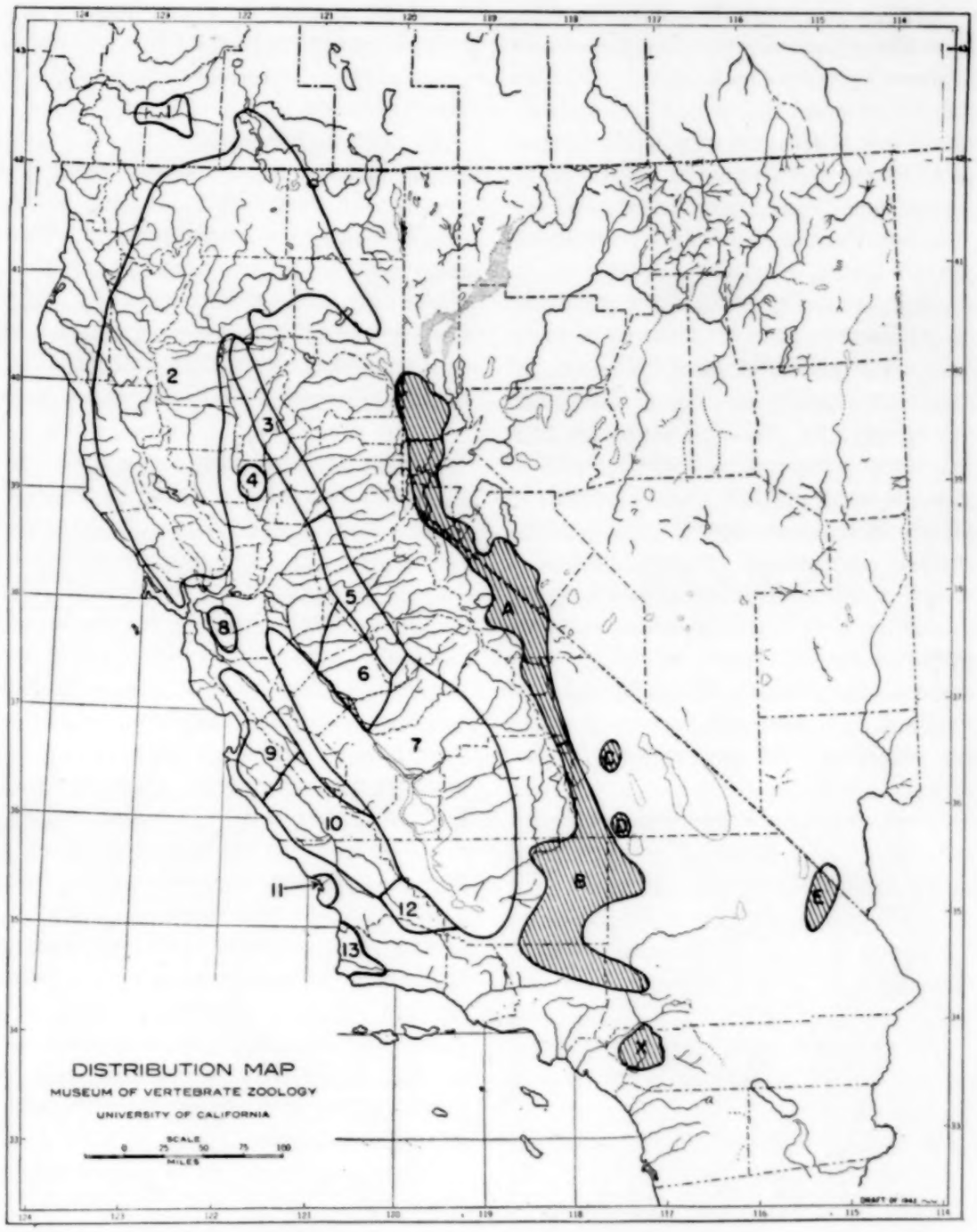


FIG. 7. Approximate ranges of the 13 races of *Dipodomys heermanni* (unshaded areas) and of the races of *Dipodomys panamintinus* (shaded areas). The form *Dipodomys stephensi*, marked with an X, probably should be regarded as a race of *D. panamintinus*. 1, *D. h. gabrielsoni;* 2, *D. h. californicus;* 3, *D. h. saxatalis;* 4, *D. h. eximius;* 5, *D. h. heermanni;* 6, *D. h. dixoni;* 7, *D. h. tularensis;* 8, *D. h. berkeleyensis;* 9, *D. h. goldmani;* 10, *D. h. jolonensis;* 11, *D. h. morroensis;* 12, *D. h. swarthi;* 13, *D. h. arenae.* A, *D. p. leucogenys;* B, *D. p. mohavensis;* C, *D. p. panamintinus;* D, *D. p. argusensis;* E, *D. p. caudatus.*

matic regimes over much of their ranges and probably have similar tolerances to temperature, rainfall, and humidity; *iliaca* and *lincolnii* are like each other in this respect even more clearly. But *georgiana* and *melodia* contrast quite evidently in habitat selection, as do *iliaca* and *lincolnii*. *Melodia* occupies wet chaparral, beach

scrub, riparian brush, fresh-water marshes, and salt-water marshes. *Georgiana* occurs only in grassy fresh-water marshes and wet meadows.

Among mammals, species of kangaroo rats of the genus *Dipodomys* afford similar examples. *Dipodomys heermanni* occurs on the Pacific coast from southern Oregon to Santa Barbara County, California, and breaks up into 13 races (fig. 7). *Dipodomys deserti* occurs from eastern central California and Nevada to northwestern Sonora and has divided into only 2 races (fig. 8). The total geographic area occupied by each species is roughly the same, although one occurs in coastal areas and the other in the deserts. *Heermanni* occupies in the total extent of its range such diversified situations as grassy hilltops, sparse shrubs, chaparral, mixed woods and brush, stony ground, and open sandy ground. *Deserti* is found in detached colonies only in deep, wind-drifted sand; it has progressed farther than *heermanni* in specialization for bipedal locomotion in sand but has narrowed its adaptations and shown less polytypic diversification.

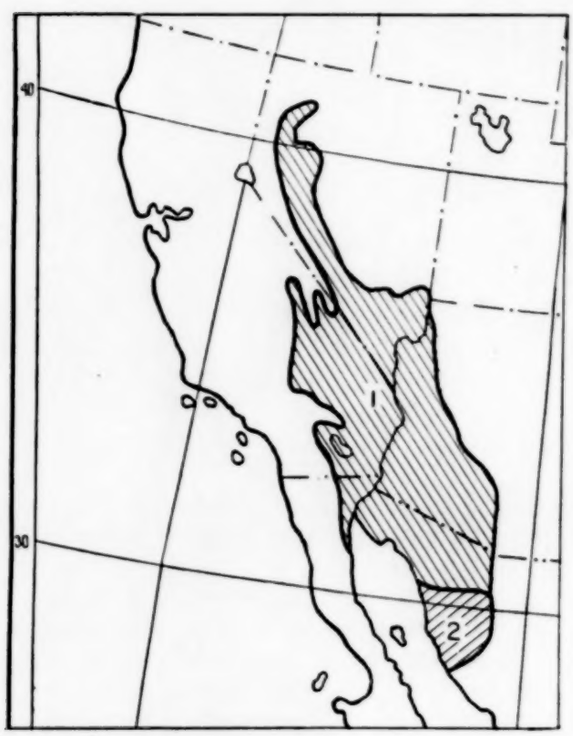


FIG. 8. Outlines of range of *Dipodomys deserti* in southwestern United States and northern México; within the range there is much local discontinuity, the species tending to occur in separate colonies. 1, *D. d. deserti;* 2, *D. d. sonoriensis.*

In part of the area occupied by *deserti* is the species *panamintinus* with 5 or 6 geographic races in a smaller total geographic range. *Panamintinus* occurs in sage brush, piñon areas, and the tree yucca belt, and on both gravelly and moderately sandy ground—a greater latitude of conditions than that tolerated by the highly adapted *deserti. Deserti* is found only in the Lower Sonoran Zone; *panamintinus* and another species, *D. microps* of the Great Basin with 14 races, both range from Lower Sonoran through Upper Sonoran; *heermanni* ranges from Lower Sonoran to Transition.

The ecologic restrictions in the several instances reviewed could operate to produce discontinuities in range in the less tolerant or less eurytopic species and hence more isolation; this in turn would restrict gene flow and give more chance for polytypic differentiation, either random or environmentally correlated. But this is apparently not the way the influences balance out in these cases. What seems to be happening is establishment of a greater difference in selection pressures in the species showing wider ecologic range and in which discontinuities may not be any more effective or frequent, indeed perhaps less so, than in the more narrowly restricted species.

This leads to a view formulated some time ago (Miller and McCabe, 1935) in connection with the genus *Passerella.* This thesis holds that *Passerella iliaca* by innate psychology (less restrictive habitat selection) may be especially given to pushing into new regions and new habitats; certainly it appears to have accomplished this. The attempt to colonize in a different area would set up new habits in the individual and throw the species under new selective influences so that racial evolution would be relatively rapid. *Passerella lincolnii,* on the other hand, by rigidly adhering to a narrow range of

ecologic conditions would not differentiate greatly. Species that are aggressive or flexible in the sense of range expansion, geographically or ecologically, and yet not too adaptable individually, form large polytypic arrays. These are the species that often receive the designation "plastic," although usually without any attempt to analyze the mechanisms lying back of the term.

From the foregoing it follows that extremely eurytopic species with great tolerance and adaptability of individuals will not trend toward extreme polytypic variation. We seem to see instances that support this idea. *Peromyscus maniculatus* on the mainland of the Pacific coast from Oregon to northern Baja California forms only 3 widespread races, although many local and quite imperfect differentiations may be noted. This species contrasts with *Peromyscus truei* in the same area which forms 7 rather distinct races. *Maniculatus* is notably lacking in ecologic restriction in this part of its continental range as every mammalogist who has trapped in the region well realizes. It ranges from desert scrub and sands to the middle pine forest belts of the mountains and frequents logs, rocks, buildings, and almost any soil type. *Truei* has a much more restricted ecologic range. It is chiefly Upper Sonoran and occurs in brush and brushy woods where there is considerable leaf litter. Also such a bird species as *Carpodacus mexicanus* in the continental western United States is distinctly eurytopic and shows little or no racial subdivision in this region.

Here then are examples quite opposite to those cited in *Passerella* and *Dipodomys*. We interpret them differently by proposing that *Peromyscus maniculatus* and *Carpodacus mexicanus* have such wide tolerances in the region concerned that they disperse freely and meet insufficiently strong selection pressures related to differences in the environments in the geographic areas through which they spread to cause development of many well-marked races. Is this explanation simply one of convenience—a device to make these examples consonant with the general thesis supported by *Passerella* and *Dipodomys?* I think the argument is not quite as fallacious as that. *Peromyscus maniculatus* and *Carpodacus mexicanus* are certainly much more extremely eurytopic than *Dipodomys heermanni* or *Passerella iliaca*.

There is, then, some reason to suppose that we can recognize a middle-ground situation that, pioneering and moderate tolerance permitting, leads to colonization of areas in which differing selection pressures will develop polytypic variation. Extreme restriction tends to block this, and extreme tolerance minimizes the differential selective pressures in diverse geographic areas.

In developing such a theory we may very easily fall into the all too-frequent practice of presenting only those especially favorable examples that support it. It is desirable, therefore, to test our hypothesis by examining a whole fauna if possible. Even though this violates our dictum of comparing close relatives, it has the advantage of taking account both of exceptions to the generalization and the supporting cases. We are in a position to do this with the bird fauna of California involving 260 breeding species. For this fauna the degree of polytypic differentiation in each species is fairly thoroughly known and the general ecologic range of each has been reviewed and tabulated (Miller, 1951). The 35 species with three or more races breeding in the state have a higher percentage (55 contrasted with 35 per cent) with a life-zonal range of 3 or more units than does the avifauna as a whole. If the 12 species that are most notably polytypic (5 or more races each) are segregated, we note an even higher proportion (65 per cent) with wide zonal range. The same general situation obtains in these species with respect to the range of ecologic formations that are occupied. But it is to be noted that occasional species with very wide ecologic range like *Euphagus cyanocephalus* are

not polytypic in agreement with the situation described earlier in other extremely eurytopic species.

The reasons for these positive correlations are not that the species are forming an array of subspecies in which each subspecies is peculiar to a single zone or to a single plant formation. The races of vertebrates are not precisely like those ecotypes of plants that tend to occur wherever a particular ecologic situation is present within the range of the species. They resemble ecotypes in that they have evolved distinctive characters adapted to ecologic conditions, but the adjustment seems to be related to a considerable range of such conditions.

## Summary

Ecologic determination, working through natural selection, is all-pervasive in the processes of speciation, including the aspects of speed of differentiation.

Cycles in numbers of individuals that are ecologically dictated, and other small-population effects that are partly ecological, promote elevation of gene combinations to significant levels of occurrence in the population and permit mass trials and recombinations. The faster and more frequent such exploratory genetic drift, the better the chance of an early attainment of a workable new combination that may be seized upon and perfected by selection.

Ecologic contrasts on borders of continents in areas of diverse topography and with pronounced hygrogradients are extraordinarily potent in race formation in terrestrial vertebrates. Without potency there can be no great speed of differentiation. The close proximity of racial differentiates, of differing population densities, greatly favors numerous and quick introgressive contacts resulting from geologic and ecologic disturbances that break down barriers. Races may be modified through exchange to arrive at favorable adaptive and compatible gene complexes and the allopatric semispecies already attained can yield species with important phyletic futures through testing under continental rigor and by borrowing improvements via introgression.

Moderate innate ecologic tolerances of species rather than either sharp restriction or eurotopy seem to favor rapid polytypic diversification. Concomitantly, moderate but not full isolation of populations favors prompt initial and subsequent evolutionary progress as made particularly clear by Sewall Wright. These "middle-ground" interpretations in which balance in the many factors of evolution is stressed might be termed the moderation thesis. Such a thesis is wholly consonant with the view that the diverse topography of continental borders promotes rapid speciation through isolative and selective mechanisms.

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# A MODEL OF A GENETIC SYSTEM WHICH LEADS TO CLOSER LINKAGE BY NATURAL SELECTION [1]

MOTOO KIMURA

*Dept. of Genetics, University of Wisconsin*

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## INTRODUCTION

It is generally assumed that linkage intensity may be modified by natural selection. Although there have been several discussions of the subject (e.g. Darlington, 1939; Fisher, 1930), no detailed mathematical analysis has been given. In the present paper a specific model in which selection leads to closer linkage will be examined.

In his 1930 book (p. 103) Fisher states, without going into detail, that "the presence of pairs of factors in the same chromosome, the selective advantage of each of which reverses that of the other, will always tend to diminish recombination, and therefore to increase the intensity of linkage in the chromosomes of that species." However, he does not discuss the ways in which the two loci are maintained in a polymorphic state, but gives a consequence (selection for decreased recombination) of such a state if it exists. Haldane (1931) has pointed out that the reversal of selective value of alleles at one locus according to which allele is present at another is not sufficient to maintain a stable polymorphism.

A specific model, in which a stable polymorphism is maintained, was proposed by Dr. P. M. Sheppard at the 1955 Cold Spring Harbor Symposium (XX: Population Genetics). Assume a locus with a pair of alleles, say $A_1$ and $A_2$, kept in balanced polymorphism by heterozygote superiority in fitness. Another pair of alleles, $B_1$ and $B_2$, are at another locus on the same chromosome, and interact with the genes in the first locus in such a way that $A_1$ is advantageous in combination with $B_1$ but is disadvantageous in combination with $B_2$, while the situation is reversed for the gene $A_2$. Then the second locus will remain polymorphic if linkage between the two loci is sufficiently close.

Under this model, close linkage would maintain a larger fraction of the fitter genotypes than loose linkage and a crossover reducing mechanism will be favored by selection.

It turns out that a full treatment of the Sheppard problem in general form is quite difficult. In the first part of this paper, therefore, I shall elaborate one specific model of the symmetrical type suggested by Sheppard to show that the polymorphism can be maintained and the type of selection on linkage intensity postulated by Fisher be effective. In the second part I shall consider more general models to point out that the main conclusion derived from the symmetrical model is still valid and applicable to such models.

## STABILITY CONDITION AND SHIFT OF EQUILIBRIUM IN THE SYMMETRICAL MODEL

The fitness of various genotypes are given in table 1 in terms of Malthusian parameters (see also Appendix I). We assume the s and t are non-negative and constant. Throughout this paper a large randomly mating population is assumed. Applying the rules for testing

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TABLE 1

| | $A_1A_1$ | $A_1A_2$ | $A_2A_2$ |
|---|---|---|---|
| $B_1B_1$ | s | t | −s |
| $B_1B_2$ | 0 | t | 0 |
| $B_2B_2$ | −s | t | s |

the stability of a selective polymorphism (Kimura, 1956), it can be shown that the proposed system can not be kept in non-trivial stable equilibrium if there is no linkage.

With complete linkage it is easily shown that the 4 types of chromosomes can not all be maintained in balanced polymorphism, though all 4 genes may be maintained; i.e., the equilibrium population may contain two chromosome types $A_1B_1$ and $A_2B_2$ or $A_1B_2$ and $A_2B_1$. The last case, however, is essentially unstable since mutation or rare recombination will break the equilibrium immediately. So we will not pay attention to this case hereafter.

Let x, y, z and u ($x + y + z + u = 1$) be the relative frequencies of the 4 types of chromosomes $A_1B_1$, $A_1B_2$, $A_2B_1$ and $A_2B_2$ respectively in the population. It is convenient to write the fitness of various genotypes in the form of table 2.

Under a continuous model of generation time, as explained in Appendix I,

TABLE 2

| | x $A_1B_1$ | y $A_1B_2$ | z $A_2B_1$ | u $A_2B_2$ |
|---|---|---|---|---|
| x $A_1B_1$ | s | 0 | t | t |
| y $A_1B_2$ | 0 | −s | t | t |
| z $A_2B_1$ | t | t | −s | 0 |
| u $A_2B_2$ | t | t | 0 | s |

the rate of change in the chromosome frequencies may be expressed by the set of differential equations:

$$\left.\begin{aligned} \dot{x} &= x(a_{x\cdot} - \bar{a}) - \rho \\ \dot{y} &= y(a_{y\cdot} - \bar{a}) + \rho \\ \dot{z} &= z(a_{z\cdot} - \bar{a}) + \rho \\ \dot{u} &= u(a_{u\cdot} - \bar{a}) - \rho \end{aligned}\right\} \quad (1)$$

where $a_{x\cdot} = sx + tz + tu$, $a_{y\cdot} = -sy + tz + tu$, $a_{z\cdot} = tx + ty - sz$ and $a_{u\cdot} = tx + ty + su$ in this specific case of table 2. The mean fitness of the population is

$$\bar{a} = a_{x\cdot}x + a_{y\cdot}y + a_{z\cdot}z + a_{u\cdot}u,$$

while $\rho$ represents the contribution by crossing over in double heterozygotes.

$$\rho = w\alpha(xu - yz),$$

where $\alpha$ is the recombination fraction between the two loci and w is the reproductive rate of the double heterozygotes defined in such a way that wdt is the probability that an $A_1A_2B_1B_2$ individual survives and reproduces in an infinitesimal time interval dt (see Appendix I).

To simplify the argument the equations (1) will be written in the following form:

$$\left.\begin{aligned} \dot{x} &= \tilde{a}_x - \rho/x \\ \dot{y} &= \tilde{a}_y + \rho/y \\ \dot{z} &= \tilde{a}_z + \rho/z \\ \dot{u} &= \tilde{a}_u - \rho/u \end{aligned}\right\} \quad (2)$$

where $\dot{x}$, $\dot{y}$, $\dot{z}$ and $\dot{u}$ are the rates of change of the logarithmic chromosome frequencies, i.e. $\dot{x} = d \log x/dt$, etc. In these formulae $\tilde{a}_x$, $\tilde{a}_y$, $\tilde{a}_z$ and $\tilde{a}_u$ denote the mean fitness of the 4 types of chromosomes measured from the average fitness of the population and will be called the average excess in fitness of these chromosome types, i.e. $\tilde{a}_x = a_{x\cdot} - \bar{a}$, etc.

For a non-trivial equilibrium, the condition $\dot{x} = \dot{y} = \dot{z} = \dot{u} = 0$ must be satisfied, that is to say,

$$\begin{aligned} \tilde{a}_x - \rho/x &= 0 \\ \tilde{a}_y + \rho/y &= 0 \\ \tilde{a}_z + \rho/z &= 0 \\ \tilde{a}_u - \rho/u &= 0. \end{aligned}$$

By virtue of symmetry, the equilibrium chromosome frequencies are expressed in a simple form:

$$\left.\begin{aligned}\hat{x} = \hat{u} &= \tfrac{1}{2}(\tfrac{1}{2} - \beta + \sqrt{\tfrac{1}{4} + \beta^2}) \\ \hat{y} = \hat{z} &= \tfrac{1}{2}(\tfrac{1}{2} + \beta - \sqrt{\tfrac{1}{4} + \beta^2})\end{aligned}\right\} \quad (3)$$

where $\beta = w\alpha/s$. At this point, the gene frequency in each locus is 50 percent. That this is the most natural gene frequency to be chosen among models in which equilibrium gene frequencies are preassigned is apparent from the very nature of the present problem, since natural selection acts somewhat symmetrically on the genetic system. The mean fitness of the population at equilibrium, which we shall designate by $\hat{\bar{a}}$, is given by

$$\hat{\bar{a}} = (s + t)/2 - 2sy. \quad (4)$$

One of the crucial parts of our problem is to determine the stability condition of this equilibrium.

Since rigorous mathematical arguments are relegated to Appendices II and III, I will here sketch rather intuitively one of the methods.

Consider a set of equilibrium chromosome frequencies $(\hat{x}, \hat{y}, \hat{z}, \hat{u})$ as a point in a 4 dimensional frequency space. Suppose we make a small displacement denoted by a vector $V_1 = (\delta\hat{x}, \delta\hat{y}, \delta\hat{z}, \delta\hat{u})$ from the equilibrium point. Then the selection pressure will tend to move the displaced chromosome frequencies in some direction. This tendency will be measured by a vector $V_2$ whose components are $(\delta\dot{\hat{x}})_e$, $(\delta\dot{\hat{y}})_e$, $(\delta\dot{\hat{z}})_e$, $(\delta\dot{\hat{u}})_e$, in which the subscript e means the value at the equilibrium. It must be noted that these elements of $V_2$ are equivalent to $[\delta(\dot{x}/x)]_e$, $[\delta(\dot{y}/y)]_e$, etc., namely, each component is weighted inversely by the corresponding gene frequency.

The necessary and sufficient condition for the stability of the equilibrium is then that the vector have a tendency to go back to the original position. More precisely, the angle made by the above two vectors must be more than 90°, or equivalently their inner product $V_1 \cdot V_2$ must always be negative:

$$V_1 \cdot V_2 < 0. \quad (5)$$

As shown in Appendix II, this leads to the condition

$$s^2 + 4\beta st < t^2, \quad (6)$$

where s, t and $\beta$ are all non negative. The above argument, convincing as it may seem, may fail to deal with the case

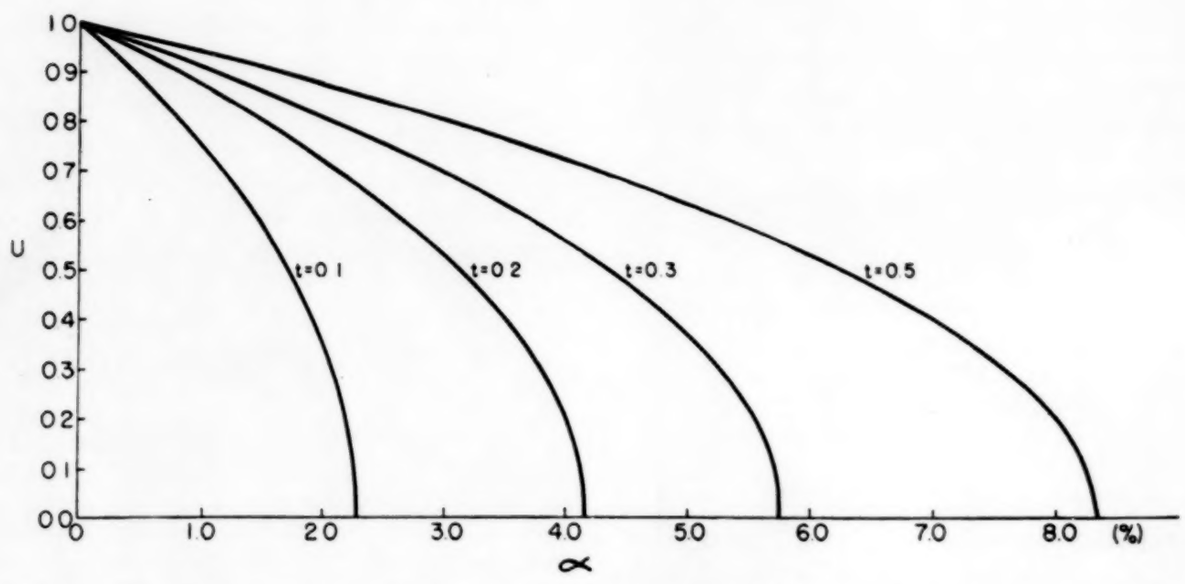


FIG. 1. The upper limit, U, of the ratio s/t as a function of the recombination fraction, $\alpha$, for selected values of t. Points to the left and below each curve lead to stable polymorphism for that particular value of t.

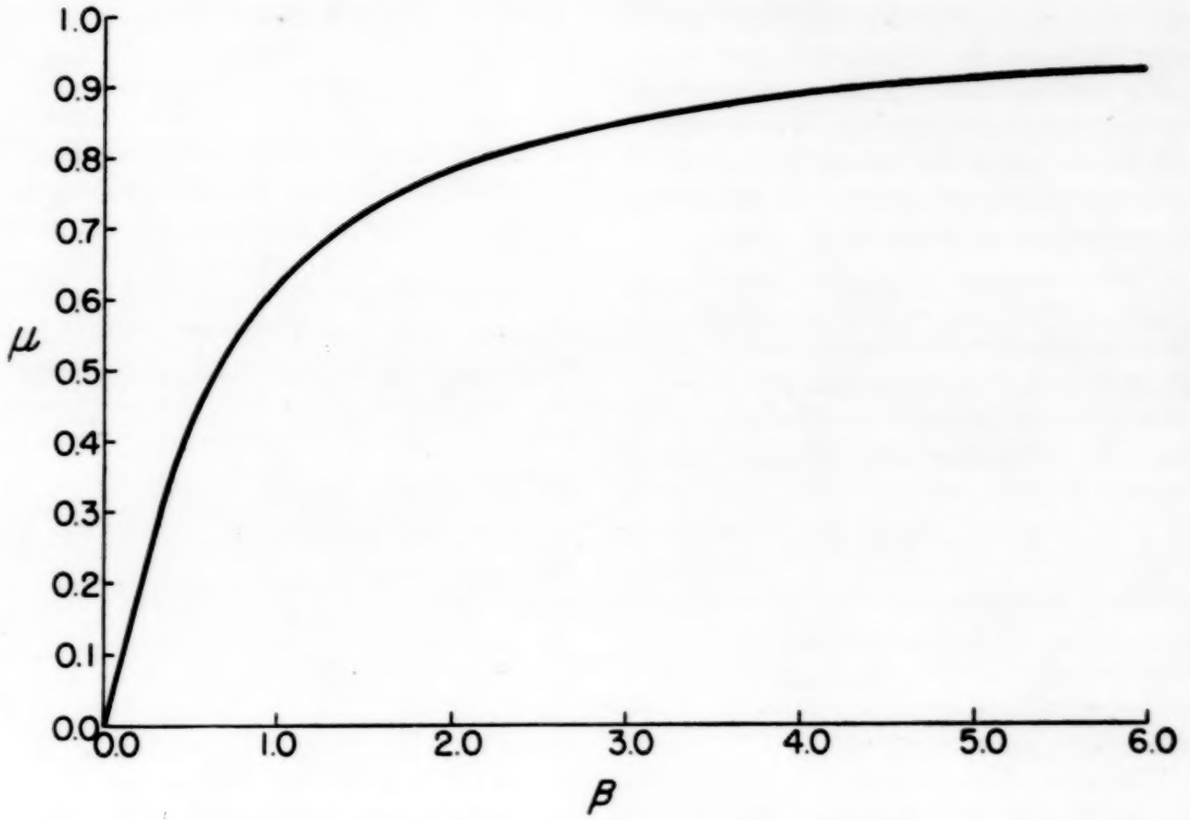


FIG. 2. The equilibrium ratio, $\mu$, of chromosomes in repulsion phase to those in coupling as a function of $\beta = w\alpha/s$. $\alpha$ = recombination fraction, s = selection intensity as defined in table 1, w is a measure of the reproductive rate of the double heterozygote.

in which the perturbed chromosome frequencies go back to the equilibrium point through a cyclically winding path. It turns out, as shown in Appendix III, that no such troublesome situation is involved in the present model and treatment by a more general method leads to exactly the same conclusion.

If we take $1 + t$ as w, the necessary and sufficient condition for stability may be written in the following form:

$$0 < s < tU, \qquad (7)$$

where

$$U = \sqrt{1 - 4(i + t)\alpha/t}.$$

From (7) we obtain the following conclusions: (i) For a given average selective advantage t of the heterozygote, the recombination fraction $\alpha$ must be smaller than $t/(4 + 4t)$, which never exceeds $1/4$. For example, if $t = 0.1$, the second locus can remain polymorphic only if there is less than 2.3% recombination with the first, or, if $t = .5$, less than 8.3%. (ii) Even within these limits there are restrictions on s if a stable polymorphism is to be maintained; the more distant the loci, the greater the restriction. Figure 1 shows this restriction in terms of the allowable upper limit (U) for the ratio s/t. For example with $t = 0.1$, s must be less than one half t, if the recombination fraction is 1.7%.

In the equilibrium population the repulsion phase ($A_2B_1$ and $A_1B_2$) is usually much less frequent than the coupling phase ($A_1B_1$ and $A_2B_2$). The ratio between the two ($\mu = \hat{y}/\hat{x}$) is determined by $\beta = w\alpha/s$ as shown in figure 2. If the linkage is very close, we have approximately $\mu = \beta$.

In general, the closer the linkage the less frequent the repulsion phase.

Suppose now that a crossover reducing mechanism, has occurred in a chromosome in coupling phase. It is easily

seen that such chromosomes will gradually increase in frequency and eventually replace the original chromosome. For example, consider the case in which a $B_1A_1$ chromosome arose from a $A_1B_1$ chromosome by inversion. If we denote the frequency of $B_1A_1$ by x′, then

$$\dot{x}' = x'\tilde{a}_x. \qquad (8)$$

As compared with the original $A_1B_1$ chromosome, it has no loss by crossing-over. At the present equilibrium point, the rate of increase in the logarithmic frequency is

$$(\dot{x}')_e = (\tilde{a}_x)_e = s\hat{y},$$

showing that the selective advantage is of the order of the recombination fraction which might be quite high (as compared with the rate of occurrence of the cross-over changing mechanism).

Through this process the population is led to the chromosome constitution consisting of 50% $B_1A_1$ and 50% $A_2B_2$. The mean fitness of the population is now $(s + t)/2$, with the gain of $2s\hat{y}$ as shown from (4). It is interesting to note that the resulting supergenes are less overdominant.

## More General Models

The main conclusions reached by the above model are by no means restricted by the assumption of the exact symmetry. For example we may assume the more general model given in table 3. If $s_1$, $s_2$, $s_3$ and $s_4$ are all positive and of approximately the same order of magnitude, while $t_1$ and $t_2$ are larger than any of them, the equilibrium population will contain predominantly coupling chromosomes $A_1B_1$ and $A_2B_2$ if linkage between the two loci is sufficiently close. Though the exact allowable upper limit of $\alpha$ is very difficult to set, it is not difficult to show if $\alpha$ is sufficiently small as compared with selective advantage or disadvantage, the equilibrium is stable.

Table 3

| | $A_1A_1$ | $A_1A_2$ | $A_2A_2$ |
|---|---|---|---|
| $B_1B_1$ | $s_1$ | $t_1$ | $-s_2$ |
| $B_1B_2$ | $\frac{s_1 - s_3}{2}$ | $\frac{t_1 + t_2}{2}$ | $\frac{s_4 - s_2}{2}$ |
| $B_2B_2$ | $-s_3$ | $t_2$ | $s_4$ |

Table 4

| | | Pink | | Yellow |
|---|---|---|---|---|
| | | $A_1A_1$ | $A_1A_2$ | $A_2A_2$ |
| Unbanded | $B_1B_1$ | $s_1$ | $s_1 + t$ | $-s_2$ |
| Unbanded | $B_1B_2$ | $s_1$ | $s_1 + t$ | $-s_2$ |
| Banded | $B_2B_2$ | $-s_3$ | $-s_3 + t$ | $s_4$ |

At this point frequencies of the repulsion chromosomes are proportional to the recombination fraction. Suppose an inversion has occurred in a coupling phase say $A_1B_1$. It is possible to show that the new chromosome with inversion $B_1A_1$, other things being equal, has selective advantage of order of the recombination fraction $\alpha$, which may be much higher than the rate of occurrence of the chromosomal rearrangement. Thus the new chromosome $B_1A_1$ will replace the original $A_1B_1$ chromosome and by so doing, the mean fitness of the population increases.

The more realistic model suggested to me by Dr. Sheppard is given in table 4. In a species of land snail, pink, unbanded ($A_1-$, $B_1-$) or yellow, banded ($A_2A_2B_2B_2$) individuals are both more advantageous than yellow, unbanded ($A_2A_2B_1-$) or pink, banded ($A_1 - B_2B_2$) individuals. Furthermore it is assumed that an individual heterozygous for $A_1$ and $A_2$ has additional advantage due to overdominance. Exactly the same type of argument is applicable to this model though to set an exact allowable upper

bound to $\alpha$ is again quite difficult due to the asymmetry involved.

## Concluding Remarks

The models given here assume that the crossover reducing influence is inherited with the chromosome influenced (as, for example, an inversion).

The effect of a crossover modifier not completely linked to the coupling chromosome is rather complicated, but would be selected with much less efficiency. These are, of course, only a few of many models that could be devised. The essential point seems to be that, if one locus already contains a mechanism for maintaining a stable polymorphism, a second linked locus may be incorporated into the system. Such a system gives a selective advantage to close linkage and thus provides a means for evolutionary adjustment of recombination values.

## Summary

As has been pointed out by various authors, frequency of recombination within a chromosome is subject to selective adjustment. In this sense, the history of the control of recombination may be regarded as a part of the history of the evolution of genetic system.

In 1930 Fisher said that with two pairs of linked loci such that $A_1$ is favored in the presence of $B_1$ while $A_2$ is favored with $B_2$ selection will act in such a way as to decrease the amount of recombination between the two loci. He did not, however, specify how a stable polymorphism of this type might be maintained. In this paper a model suggested by Sheppard is examined. It is shown that, if the first locus is maintained in balanced polymorphism by heterozygote superiority in fitness, the second locus will remain polymorphic if linkage is sufficiently close. Under this condition an inversion (or other crossover reducing mechanism) will be favored by selection and, other things being equal, will eventually be established in the population.

## Appendix I

*Derivation of the set of equations (1) based on the model of continuous generation time.*

Consider a very large randomly mating population. We assume that the population is continuous in time, that is, reproduction and death of the members of this population go on uniformly throughout the year. To facilitate concise mathematical argument we shall choose slightly different notations from the ones given in section 2. First we define the two quantities denoted by $b_{ijkl}$ and $d_{ijkl}$ in such way that

$b_{ijkl}\Delta t$: Probability that a randomly chosen individual of genotype $A_iA_jB_kB_l$ survives and reproduces in a small time interval $\Delta t$. (i, j, k, l = 1, 2)

$d_{ijkl}\Delta t$: Probability that a randomly chosen individual of genotype $A_iA_jB_kB_l$ dies in the interval $\Delta t$ without producing offspring in that interval.

Then the fitness of $A_iA_jB_kB_l$ is defined by

$$a_{ijkl} = b_{ijkl} - d_{ijkl}.$$
$$(a_{ijkl} = a_{jikl} = a_{jilk})$$

Any quantities of order $(\Delta t)^2$ will be neglected. The fitness so defined gives the geometric rate of increase or decrease of the number of individuals with genotype $A_iA_jB_kB_l$ and following Fisher (1930) will be called the fitness of the genotype measured in Malthusian parameters.

If we designate by $n_{ik}$ the number of $A_iB_k$ chromosomes in the population and by N the total number of chromosomes ($N = \sum_{ik} n_{ik}$), the frequency of the $A_iB_k$ is given by

$$x_{ik} = n_{ik}/N. \qquad (\sum_{ik} x_{ik} = 1)$$

Let us first consider the increase in the number of the chromosome $A_1B_1$ in the

small time interval $\Delta t$. It is not difficult to see that

$$\begin{aligned}\Delta n_{11} = {} & b_{1111}\Delta t N x_{11}^2 + b_{1112}\Delta t N x_{11}x_{12} \\ & + b_{1211}\Delta t N x_{11}x_{21} \\ & + b_{1212}\Delta t N x_{11}x_{22}(1-\alpha) \\ & + b_{1212}\Delta t N x_{21}x_{12}\alpha \\ & - d_{1111}\Delta t N x_{11}^2 \\ & - d_{1112}\Delta t N x_{11}x_{12} \\ & - d_{1211}\Delta t N x_{11}x_{21} \\ & - d_{1212}\Delta t N x_{11}x_{22},\end{aligned}$$

where $\alpha$ is the recombination fraction. Divide both sides by $N\Delta t$ and note that $a = b - d$, then

$$\frac{1}{N}\frac{\Delta n_{11}}{\Delta t} = x_{11}a_{1\cdot 1\cdot} - b_{1212}\alpha D$$

where $a_{1\cdot 1\cdot} = a_{1111}x_{11} + a_{1112}x_{12} + a_{1211}x_{21} + a_{1212}x_{22}$ and $D = x_{11}x_{22} - x_{12}x_{21}$.

Similarly we can derive

$$\frac{1}{N}\frac{\Delta n_{12}}{\Delta t} = x_{12}a_{1\cdot 2\cdot} + b_{1212}\alpha D$$

$$\frac{1}{N}\frac{\Delta n_{21}}{\Delta t} = x_{21}a_{2\cdot 1\cdot} + b_{1212}\alpha D$$

$$\frac{1}{N}\frac{\Delta n_{22}}{\Delta t} = x_{22}a_{2\cdot 2\cdot} - b_{1212}\alpha D$$

Therefore, if we note that $N = n_{11} + n_{12} + n_{21} + n_{22}$,

$$\frac{1}{N}\frac{\Delta N}{\Delta t} = \bar{a},$$

where $\bar{a} = x_{11}a_{1\cdot 1\cdot} + x_{12}a_{1\cdot 2\cdot} + x_{21}a_{2\cdot 1\cdot} + x_{22}a_{2\cdot 2\cdot}$. Thus

$$\begin{aligned}\frac{\Delta x_{11}}{\Delta t} = \frac{\Delta}{\Delta t}\left(\frac{n_{11}}{N}\right) &= \frac{\frac{\Delta n_{11}}{\Delta t}N - n_{11}\frac{\Delta N}{\Delta t}}{N^2} \\ &= \frac{1}{N}\frac{\Delta n_{11}}{\Delta t} - \frac{n_{11}}{N}\left(\frac{1}{N}\frac{\Delta N}{\Delta t}\right) \\ &= x_{11}a_{1\cdot 1\cdot} - \alpha b_{1212}D - x_{11}\bar{a}.\end{aligned}$$

Taking the limit $\Delta t \to 0$ and writing $dx_{11}/dt$ with the Newtonian symbol $\dot{x}_{11}$, we have

$$\dot{x}_{11} = x_{11}(a_{1\cdot 1\cdot} - \bar{a}) - \rho,$$

where $\rho = \alpha b_{1212}D$. Similarly we have

$$\dot{x}_{12} = x_{12}(a_{1\cdot 2\cdot} - \bar{a}) + \rho$$

$$\dot{x}_{21} = x_{21}(a_{2\cdot 1\cdot} - \bar{a}) + \rho$$

$$\dot{x}_{22} = x_{22}(a_{2\cdot 2\cdot} - \bar{a}) - \rho.$$

If we replace $x_{11}$, $x_{12}$, $x_{21}$, and $x_{22}$ respectively by new symbols x, y, z, and u, $a_{1\cdot 1\cdot}$, $a_{1\cdot 2\cdot}$, $a_{2\cdot 1\cdot}$, and $a_{2\cdot 2\cdot}$ by $a_x$., $a_y$., $a_z$. and $a_u$., and finally $b_{1212}$ by w, we have the equations (1) in general form.

## Appendix II

*Derivation of condition (6) in section 2.*

Given

$$\begin{aligned}V_1 \cdot V_2 = {} & (\delta\hat{x})(\delta\mathring{x})_e + (\delta\hat{y})(\delta\mathring{y})_e \\ & + (\delta\hat{z})(\delta\mathring{z})_e + (\delta\hat{u})(\delta\mathring{u})_e < 0,\end{aligned}$$

we want to derive the condition (6) in section 2, i.e. $s^2 + 4\beta st < t^2$. If we use the relations:

$$(\delta\mathring{x})_e = \left(\frac{\partial\mathring{x}}{\partial x}\right)_e \delta\hat{x} + \left(\frac{\partial\mathring{x}}{\partial y}\right)_e \delta\hat{y} + \left(\frac{\partial\mathring{x}}{\partial z}\right)_e \delta\hat{z} + \left(\frac{\partial\mathring{x}}{\partial u}\right)_e \delta\hat{u},$$

$$(\delta\mathring{y})_e = \left(\frac{\partial\mathring{y}}{\partial x}\right)_e \delta\hat{x} + \left(\frac{\partial\mathring{y}}{\partial y}\right)_e \delta\hat{y} + \left(\frac{\partial\mathring{y}}{\partial z}\right)_e \delta\hat{z} + \left(\frac{\partial\mathring{y}}{\partial u}\right)_e \delta\hat{u}, \quad \text{etc.},$$

where

$$\left(\frac{\partial\mathring{x}}{\partial x}\right)_e = 2s\hat{y} - t - w\alpha\mu^2, \qquad \left(\frac{\partial\mathring{y}}{\partial x}\right)_e = -2s\hat{x} - t + w\alpha\mu^{-1}$$

$$\left(\frac{\partial\mathring{x}}{\partial y}\right)_e = 2s\hat{y} - t + w\alpha, \qquad \left(\frac{\partial\mathring{y}}{\partial y}\right)_e = -2s\hat{x} - t - w\alpha\mu^{-2}$$

$$\left(\frac{\partial\mathring{x}}{\partial z}\right)_e = 2s\hat{y} + w\alpha, \qquad \left(\frac{\partial\mathring{y}}{\partial z}\right)_e = 2s\hat{y} - w\alpha$$

$$\left(\frac{\partial\mathring{x}}{\partial u}\right)_e = -2s\hat{x} - w\alpha, \qquad \left(\frac{\partial\mathring{y}}{\partial u}\right)_e = -2s\hat{x} + c\mu^{-1}, \quad \text{etc.},$$

in which $\mu = \hat{y}/\hat{x}$, we can express $V_2$ in terms of $\delta\hat{x}$, $\delta\hat{y}$, $\delta\hat{z}$ and $\delta\hat{u}$. Thus $V_1 \cdot V_2$ is expressed as a quadratic form in $\delta\hat{x}$, $\delta\hat{y}$, etc. However the 4 chromosome frequencies are not independent and $\delta\hat{u} = -\delta\hat{x} - \delta\hat{y} - \delta\hat{z}$. Substituting this in the quadratic form we obtain a new quadratic form in three variables $\delta\hat{x}$, $\delta\hat{y}$ and $\delta\hat{z}$, the matrix of which, after dividing by $s^3$, is

$$T = \begin{bmatrix} 2(1-\lambda+\beta-\beta\mu^2) & 1-2\lambda+\beta-\beta\mu^2 & 1+\beta-\beta\mu^2 \\ 1-2\lambda+\beta-\beta\mu^2 & -2\lambda-\beta(\mu^{-2}+\mu^{-1}+\mu+\mu^2) & 1-\beta(\mu^{-1}+1+\mu+\mu^2) \\ 1+\beta-\beta\mu^2 & 1-\beta(\mu^{-1}+1+\mu+\mu^2) & -\beta(\mu^{-2}+\mu^{-1}+\mu+\mu^2) \end{bmatrix}$$

where $\lambda = t/s$ and $\beta = w\alpha/s$. The condition $V_1 \cdot V_2 < 0$ is equivalent to the condition that a quadratic form associated with T is negative definite. From this we obtain the following three conditions with respect to $\lambda$:

(i) $\lambda > 1 + \beta - \beta\mu^2$

(ii) $\lambda > \dfrac{(1 + \beta - \beta\mu^2)\{1 + \beta(2\mu^{-2} + 2\mu^{-1} + 1 + 2\mu + \mu^2)\}}{2\beta(\mu^{-2} + \mu^{-1} + \mu + \mu^2)}$

(iii) $\lambda > \dfrac{(1 + \beta - \beta\mu^2)(1 - \beta + \beta\mu^{-2})}{\beta(\mu^{-2} - 2 + \mu^2)}$.

The last condition turns out to be the strongest and if we substitute

$$\mu = \hat{y}/\hat{x} = \frac{1 + 2\beta - \sqrt{1 + 4\beta^2}}{1 - 2\beta + \sqrt{1 + 4\beta^2}}$$

in (iii), we obtain

$$s < (\sqrt{1 + 4\beta^2} - 2\beta)t;$$

which is equivalent to

$$s^2 + 4\beta st < t^2$$

if $s > 0$ and $t > 0$. If we note $\beta = w\alpha/s$, this may also be written in the form $s^2 + 4w\alpha t < t^2$.

## Appendix III

*General treatment of the stability condition with the demonstration that no spirally winding paths are involved.*

We start from the set of differential equation (1) given in section 2. Let $\delta x$, $\delta y$, $\delta z$ and $\delta u$ be the small deviations of chromosome frequencies x, y, z and u from their respective equilibrium frequencies $\hat{x}$, $\hat{y}$, $\hat{z}$ and $\hat{u}$. Then we have

$$\begin{bmatrix} \dot{\delta\hat{x}} \\ \dot{\delta\hat{y}} \\ \dot{\delta\hat{z}} \\ \dot{\delta\hat{u}} \end{bmatrix} = \begin{bmatrix} s\hat{y} & \frac{c}{2} & t\hat{x} + \frac{c}{2} & (t-s)\hat{x} \\ 0 & -s\hat{x} - \frac{c}{2} & (t+s)\hat{y} - \frac{c}{2} & t\hat{y} \\ t\hat{y} & (t+s)\hat{y} - \frac{c}{2} & -s\hat{x} - \frac{c}{2} & 0 \\ (t-s)\hat{x} & t\hat{x} + \frac{c}{2} & \frac{c}{2} & s\hat{y} \end{bmatrix} \begin{bmatrix} \delta x \\ \delta y \\ \delta z \\ \delta u \end{bmatrix}$$

where $c = \alpha w$ and $\hat{\delta\dot{x}}$ means $(d(\delta x)/dt)_e$ etc. Since the 4 chromosome frequencies are not independent, we substitute

$$\delta u = -\delta x - \delta y - \delta z$$

in the above equation to get

$$\begin{bmatrix} \hat{\delta\dot{x}} \\ \hat{\delta\dot{y}} \\ \hat{\delta\dot{z}} \end{bmatrix} = \begin{bmatrix} \frac{s}{2} - t\hat{x} & (s-t)\hat{x} + \frac{c}{2} & s\hat{x} + \frac{c}{2} \\ -t\hat{y} & -s\hat{x} - t\hat{y} - \frac{c}{2} & s\hat{y} - \frac{c}{2} \\ t\hat{y} & (s+t)\hat{y} - \frac{c}{2} & -s\hat{x} - \frac{c}{2} \end{bmatrix} \begin{bmatrix} \delta\hat{x} \\ \delta\hat{y} \\ \delta\hat{z} \end{bmatrix}$$

For the derivation of the above equations, the following relations are found to be very useful:

$2s\hat{x}\hat{y} = c(\hat{x} - \hat{y})$, $2s\hat{x}^2 = s\hat{x} - c(\hat{x} - \hat{y})$, $2s\hat{y}^2 = s\hat{y} - c(\hat{x} - \hat{y})$ and $\hat{x} + \hat{y} = 1/2$.

The necessary and sufficient condition that the equilibrium is stable is that the real parts of all the characteristic roots of the matrix in the above equation be negative (see Bellman, 1953, p. 25).

After tedious but straightforward calculation we get the characteristic equation in the following form:

$$\lambda^3 + \frac{t+v}{2}\lambda^2 + \left\{\frac{(v-c)t}{2} - \frac{s^2}{4}\right\}\lambda - \frac{v}{8}(s^2 - tv + 2ct) = 0, \quad (\#1),$$

where $v = \sqrt{s^2 + 4c^2}$. Here we note that s, t, c and v are all non negative quantities. Let $\lambda = X/2$, then (#1) becomes

$$X^3 + (t+v)X^2 + \{2(v-c)t - s^2\}X - v(s^2 - tv + 2ct) = 0. \quad (\#2)$$

First we try to show that all the roots of (#2) and therefore all the roots of (#1) are real. If we put $X = Y - (t+v)/3$, we obtain the cubic equation of the form

$$Y^3 + pY + q = 0. \quad (\#3)$$

Now we proceed to show that the discriminant of (#3)

$$\Delta = q^2/4 + p^3/27$$

is negative. Calculations involved are again tedious but straightforward. They lead to

$$\frac{108\Delta}{c^2} = -16s^2t^2 + 112c^2t^2 + 64cs^2t - 16ct^3 - 4t^4 - 128c^3t - 64c^2s^2 + v(t-2c)^2 16t.$$

The last term is non negative and if we apply the inequality

$$v = \sqrt{s^2 + 4c^2} \leqq s + 2c,$$

we get

$$108\Delta \leqq -4c^2(t-2c)^2(t-2s)^2 \leqq 0.$$

Thus

$$\Delta \leqq 0$$

and all the roots of (#3) and therefore all the roots of (#1) are real. This is enough to show that there are no spirally winding paths to the equilibrium gene frequency.

Furthermore, once we know that no imaginary roots are involved, the necessary and sufficient condition that the real parts of all the roots of (#1) be negative can be worked out very simply. Namely we require that coefficients of $x^2$, $x^1$, and $x^0$ in (#2) are all positive.

$$\begin{aligned} t + v &> 0 \\ 2(v-c)t - s^2 &> 0 \\ -v(s^2 - tv + 2ct) &> 0. \end{aligned}$$

It may be immediately seen that the last inequality is the strongest one and

if we note $v = \sqrt{s^2 + 4c^2}$, we get

$$t^2 > s^2 + 4ct$$

which is exactly the same condition obtained in Appendix II since $c = \alpha w$.

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# CHROMOSOMAL POLYMORPHISM AND SEXUAL ISOLATION IN SIBLING SPECIES OF THE BOCAINENSIS SUBGROUP OF DROSOPHILA [1]

FRANCISCO M. SALZANO

*Instituto de Ciências Naturais, Universidade do Rio Grande do Sul, Pôrto Alegre, Rio Grande do Sul, Brazil*

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## INTRODUCTION

Carson (1954) showed that under the taxonomic designation of *Drosophila bocainensis* Pavan and da Cunha, 1947, it is possible to distinguish three reproductively isolated Mendelian populations. These populations he described as species, although two of them were morphologically indistinguishable, and the third distinguishable only in the males. Carson named them *D. bocainensis* (sensu stricto), *D. parabocainensis* and *D. bocainoides*, respectively. He showed also that *D. bocainensis* and *D. parabocainensis* cross freely and produce abundant fertile offspring in the laboratory. No hybrids were, however, obtained between these species and *D. bocainoides*.

The present work describes experiments made to test further the possibility of gene exchange between these species. An examination of the salivary gland chromosomes, and a study of the sexual isolation that exists among several geographic strains have been made. The results of the studies of the chromosomal polymorphism are considered in the light of the hypothesis advanced by da Cunha, Burla and Dobzhansky (1950) and Dobzhansky, Burla and da Cunha (1950), namely that the amount of the polymorphism is a function of the variety of ecological niches which a population has mastered.

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## MATERIAL AND METHODS

The bocainensis subgroup belongs to the willistoni group of Drosophila. This group is composed of eleven species, four of which constitute the willistoni group of sibling species (*D. willistoni, D. paulistorum, D. tropicalis* and *D. equinoxialis*), and three the bocainensis subgroup (*D. bocainensis, D. parabocainensis* and *D. bocainoides*). The other species are: *D. fumipennis, D. capricorni, D. nebulosa* and *D. sucinea* (Patterson and Stone, 1952; Carson, 1954). The individuals studied were collected by the method of Pavan and da Cunha (1947) from the localities of Ponta Grossa, Emboaba, Bexiga, Muitos Capões and Feliz in the state of Rio Grande do Sul; Paranai in the state of Paraná; Cantareira, in the state of São Paulo, and El Destino, in Argentina. The females of *D. bocainensis, D. parabocainensis* and *D. bocainoides* were, whenever possible, separated from the males after collection, each placed in individual culture bottles, and allowed to produce offspring. When mature larvae appeared, the salivary glands of one or more larvae from each culture were prepared in temporary acetic orcein mounts, and their chromosomes examined. For statistical purposes, the gene arrangements were scored in only a single larva from each culture. Some of the inversions recorded here were described by Carson (1954) and the others will be described elsewhere (Salzano, 1956).

For the experiments dealing with sexual isolation, the method followed was the "multiple choice" technique. Ten females, five from one species and five from the

other in the interspecific crosses, or different strains of the same species in the intraspecific ones, were placed in 7.5 × 5 cm vials with five males from one of the species or strains tested. All individuals were virgin and six days old. For the distinction of females of the two species or strains studied the procedure used was to cut off one of the halteres of the flies from one of the species or strain. This was done with a slight etherization, three days after the emergence of the imagos. In order to make the treatment uniform, the females whose halteres had not been cut off were etherized as well. With the same objective (uniformity of treatment), the cutting off the halteres was made alternatively in one or another species or strain—in a vial, for instance, the species whose halteres were cut off was *D. bocainensis;* in another (of the same series) was *D. parabocainensis*—no difference in the behavior of the flies with or without halteres, however, was found. The vials with the males and females crossed were kept for two days in a constant temperature room (20 ± 1° C), after which the females were dissected in physiological salt solution and their ventral receptacles and spermathecae examined for the presence of sperm.

The species studied (*D. bocainensis, D. parabocainensis* and *D. bocainoides*) presented certain peculiarities, in relation to their rearing, that are worth mentioning. Thus, only about 50% of the females collected in nature produce offspring in the laboratory. The remaining 50% can be reared if they are kept at temperatures near or below 20° C. Above this temperature it is impossible to cultivate these flies. Their salivary gland chromosomes are relatively easy to study, since, with the exception of the left arm of chromosome 2, all of them spread fairly well in the preparations studied.

## Geographic Distribution and Relative Abundance

The bocainensis subgroup of Drosophila has a very large known distribution area. Specimens from this subgroup were collected in several places in Brazil and in one place in Argentina. Generally, however, these flies occurred in very low frequencies in collections made using banana baits. Pavan (1952) presented evidence that this rareness could be better explained by the assumption that they are not well attracted by this kind of bait, rather than assuming that their populations were effectively small. Cytological studies of

Table 1. *Relative frequencies of the three species that belong to the bocainensis subgroup in collections made in several Brazilian localities and in one locality of Argentina*

| Locality | Total | Percentages | | |
|---|---|---|---|---|
| | | *D. bocainensis* | *D. parabocainensis* | *D. bocainoides* |
| Rio Grande do Sul, 1952–1955 | | | | |
| Muitos Capões | 64 | 0.00 | 100.00 | 0.00 |
| Feliz | 275 | 49.09 | 50.91 | 0.00 |
| Emboaba | 91 | 72.53 | 27.47 | 0.00 |
| Ponta Grossa | 75 | 92.00 | 8.00 | 0.00 |
| Bexiga | 15 | 60.00 | 40.00 | 0.00 |
| All localities | 520 | 53.65 | 46.35 | 0.00 |
| Paraná, 1953 | | | | |
| Paranai | 7 | 100.00 | 0.00 | 0.00 |
| São Paulo, 1954 | | | | |
| Cantareira* | 49 | 61.22 | 0.00 | 38.78 |
| Argentina, 1954 | | | | |
| El Destino | 6 | 100.00 | 0.00 | 0.00 |

* Among flies of a stock sent in 1952 by Dr. A. B. da Cunha there were specimens of *D. parabocainensis.*

specimens coming from the states of Minas Gerais, São Paulo, Paraná, Rio Grande do Sul and those from Argentina were made by the present writer and by Carson (1954).

The results obtained now are summarized on table 1. An inspection of this table shows that in the state of Rio Grande do Sul only two of the species, *D. bocainensis* and *D. parabocainensis,* are found; if all the data concerning the different localities in this state are summed up, it is found that the frequency of each does not differ significantly from 50%. If, however, each locality is considered separately, it can be seen that in three *D. bocainensis* is more frequent, and *D. parabocainensis* more frequent in two of them. In the

TABLE 2. *Frequencies (per cent) of heterozygous inversions and mean numbers of heterozygous inversions per individual* D. bocainensis *in several Brazilian localities and in one locality of Argentina*

| Inversions | Localities | | | | | | |
|---|---|---|---|---|---|---|---|
| | Feliz | P. Grossa | Emboaba | Cantareira | Bexiga | Paranai | El Destino |
| Chromosome XL | | | | | | | |
| None | 95.89 | 97.73 | 94.44 | 64.29 | 100.00 | 100.00 | 100.00 |
| XL-Bb | 4.11 | 2.27 | 5.56 | 35.71 | — | — | — |
| Chromosome XR | | | | | | | |
| None | 47.94 | 50.00 | 47.22 | 28.57 | 100.00 | 66.67 | 50.00 |
| XR-Aa | 4.11 | — | 2.78 | 7.14 | — | — | — |
| XR-Bb | 47.94 | 50.00 | 50.00 | 64.29 | — | 33.33 | 50.00 |
| Chromosome 2R | | | | | | | |
| None | 97.25 | 91.30 | 87.23 | 100.00 | 66.67 | 100.00 | 66.67 |
| 2R-Bb | 2.75 | 8.70 | 12.77 | — | 33.33 | — | 33.33 |
| Chromosome 2L | | | | | | | |
| None | 84.40 | 86.96 | 89.36 | 50.00 | 100.00 | 85.71 | 100.00 |
| 2L-Aa | 6.42 | 7.25 | 6.38 | 38.46 | — | — | — |
| 2L-Bb | 13.76 | 11.59 | 8.51 | 34.62 | — | 14.29 | — |
| 2L-Cc | 12.84 | 11.59 | 6.38 | 23.08 | — | — | — |
| Chromosome 3 | | | | | | | |
| None | 19.27 | 14.49 | 12.77 | 7.69 | — | 14.29 | 33.33 |
| 3-Aa | 37.61 | 37.68 | 51.06 | 34.62 | 33.33 | 14.29 | 33.33 |
| 3-Bb | 35.78 | 39.13 | 53.19 | 19.23 | 33.33 | 14.29 | 33.33 |
| 3-Cc | 23.85 | 26.09 | 14.89 | 42.31 | 66.67 | 42.86 | 33.33 |
| 3-Dd | 43.12 | 50.72 | 40.43 | 42.31 | 100.00 | 57.14 | 66.67 |
| 3-Ee | 1.83 | — | 2.13 | 7.69 | — | — | — |
| 3-Ff | 1.83 | 4.35 | 2.13 | 11.54 | — | — | — |
| 3-Gg | 31.19 | 37.68 | 42.55 | 50.00 | 33.33 | 14.29 | 33.33 |
| 3-Hh | 34.86 | 33.33 | 46.81 | 42.31 | 33.33 | 28.57 | 33.33 |
| 3-Ii | — | 4.35 | — | 7.69 | — | — | — |
| 3-Jj | 30.28 | 33.33 | 40.43 | 38.46 | 33.33 | 28.57 | 33.33 |
| 3-Ll | — | — | 2.13 | — | — | — | — |
| 3-Mm | 24.77 | 31.88 | 19.15 | 7.69 | 66.67 | 57.14 | — |
| 3-Nn | 58.71 | 66.67 | 63.83 | 46.15 | 100.00 | 85.71 | 33.33 |
| Mean per individual | ♀ =4.12 ±0.30 | ♀ =4.57 ±0.35 | ♀ =4.78 ±0.41 | ♀ =5.07 ±0.70 | — | — | — |
| | ♂ =3.58 ±0.38 | ♂ =4.04 ±0.49 | ♂ =3.91 ±0.84 | ♂ =5.00 ±0.80 | — | — | — |
| Flies tested | ♀ =73 | ♀ =44 | ♀ =36 | ♀ =14 | ♀ =2 | ♀ =6 | ♀ =2 |
| | ♂ =36 | ♂ =25 | ♂ =11 | ♂ =12 | ♂ =1 | ♂ =1 | ♂ =1 |

localities outside of Rio Grande do Sul, *D. bocainensis* was the only species found in Paranai and El Destino (where, however, the numbers of flies examined were small—see table 1) and at Cantareira *D. bocainensis* and *D. bocainoides* were found, the first presenting a higher frequency in relation to the second.

Our results in a general way confirm those presented by Carson (1954). *D. bocainensis* is the commonest and most widespread species of the subgroup. *D. parabocainensis* is more frequent in localities with cool climates, whereas *D. bocainoides* is characteristic of the superhumid coastal rainforests of São Paulo.

### Inversion Frequencies in Natural Populations

Table 2 presents the frequencies of the different heterozygous inversions found in populations of *D. bocainensis* sampled in several Brazilian localities and in one locality of Argentina. The data shown in the three right-hand columns, concerning the localities of Bexiga, Paranai and El Destino, are presented only for comparative purposes. Since the number of individuals analyzed there was very small, these localities were not considered in the quantitative study of the results obtained.

Some of the inversions did not present differences in their frequencies in the localities studied, but some, as inversion 3 – Bb ($\chi^2 = 8.71$, d. f. = 3, $P < 0.05$), clearly did. In some cases, the expected numbers for some classes were very small; as a consequence, the frequencies of some inversions had to be analyzed jointly. 2L – Bb and 2L – Cc were in this group, and their combined frequencies showed significant differences in the localities tested ($\chi^2 = 14.00$, d. f. = 3, $P < 0.01$). The same is true for the combination between the frequencies of individuals without inversions in chromosome 2L and the carriers of inversion 2L – Aa ($\chi^2 = 45.81$, d. f. = 3, $P < 0.001$) and those without inversions in chromosome XR with the carriers of inversion XL – Bb ($\chi^2 = 8.33$, d. f. = 3, $P < 0.05$).

As shown in table 2, all the inversions localized in the left arm of chromosome 2 present their highest frequencies at Cantareira, and lowest at Emboaba, with Ponta Grossa and Feliz presenting intermediate values. The gene arrangement XL – Bb also, has its highest frequency at Cantareira, but its lowest percentage is observed at Ponta Grossa. With inversion 3 – Bb the opposite situation to what has happened with inversions in chromosome 2L is true, i.e., its highest frequency was observed at Emboaba, and the lowest at Cantareira. It is evident that differences exist between the populations of the state of São Paulo and those from Rio Grande do Sul. These results are in agreement with those obtained by Carson (1954), who also noted the difference in the inversions in the populations of Rio Grande do Sul and of São Paulo, the individuals belonging to the localities in the last state presenting generally, in his data, a higher percentage of inversions. The results obtained with inversion 3 – Nn must be emphasized. As can be seen, this inversion is present in high numbers in the localities studied. Its frequencies, indeed, are significantly higher than 50% ($\chi^2 = 11.18$, d. f. = 1, $P < 0.001$).

If now, in the same table, the mean number of heterozygous inversions per individual is calculated, it can be seen that the values obtained are all in the neighborhood of 4.00. None differ significantly from this number.

In contrast with *D. bocainensis*, *D. parabocainensis* presents a very limited chromosomal polymorphism. Only two different inversions were found in this species. The frequencies of each, as well as the mean number of heterozygous inversions per individual, are shown in table 3. One of the inversions (2L – Dd) is very rare, having been found only once at Muitos Capões. The other is present in the several localities tested, but the frequencies obtained do not differ significantly among themselves. As far as the mean number of heterozygous inversions per individual is concerned, the recorded

TABLE 3. *Frequencies (per cent) of heterozygous inversions and mean numbers of heterozygous inversions per individual* D. parabocainensis *in different localities in Rio Grande do Sul*

| Inversions | Localities | | | | |
|---|---|---|---|---|---|
| | Feliz | M. Capões | Emboaba | Bexiga | P. Grossa |
| Chromosome 2R | | | | | |
| None | 73.28 | 60.94 | 73.33 | 83.33 | 60.00 |
| 2R-Aa | 26.72 | 39.06 | 26.67 | 16.67 | 40.00 |
| Chromosome 2L | | | | | |
| None | 100.00 | 98.44 | 100.00 | 100.00 | 100.00 |
| 2L-Dd | — | 1.56 | — | — | — |
| Mean per individual | 0.27±0.04 | 0.41±0.07 | 0.27±0.12 | 0.17 | 0.40 |
| Flies tested | 116 | 64 | 15 | 6 | 5 |

values are 0.27, 0.27 and 0.41 in the three localities where good samples could be obtained. The differences among them are not significant.

Owing to the fact that there is no *D. bocainoides* in the state of Rio Grande do Sul, only 10 individuals could be analyzed in this species, all collected at Cantareira. Three of them presented the inversion 2L – Ee and two the inversion 2R –Cc.

## SEXUAL ISOLATION

The results of the experiments dealing with sexual isolation in the three species of the bocainensis subgroup are summarized on figure 1 and table 4. Strains coming from the locality of Feliz for *D. bocainensis* and *D. parabocainensis,* and from Cantareira, for *D. bocainoides,* were chosen as the centers of the crosses in the tests made. These tests involved: a) Individuals of the same species, coming from different localities; b) individuals of different species, coming from different localities; c) individuals of different species, coming from the same locality.

The results presented in table 4 show first that in the intraspecific crosses, with strains coming from different localities (*D. parabocainensis* from Feliz × *D. parabocainensis* from Emboaba; *D. bocainensis* from Feliz × *D. bocainensis* from Emboaba), no significant differences were found in the frequency of insemination between individuals coming from the same or from different localities. The coefficients of joint isolation (Levene, 1949) in these cases were $-0.11 \pm 0.06$ and $-0.06 \pm 0.07$, respectively.

Turning now to the interspecific crosses, it can be seen that the males of *D. bocainensis* and *D. parabocainensis,* even when they can choose between females of their own and of the foreign species, inseminate a relatively high percentage of the latter. The frequency of interspecific inseminations in the crosses varied between 21.50% and 62.89%. In contrast with this, the interspecific crosses involving *D. bocainensis* × *D. bocainoides* and *D. parabocainensis* × *D. bocainoides* presented a very low percentage of insemination (from zero to 1.02%). Meanwhile, in spite of the fact that the frequency of insemination is high in the tests made between *D. bocainensis* and *D. parabocainensis,* almost all of them indicate that a significantly higher percentage of individuals of the same species cross with each other, rather than with individuals of the other species. In fact, only in one case this did not happen: in the cross between *D. parabocainensis* from Feliz with *D. bocainensis* from Ponta Grossa (K 1 and $2 = 0.12 \pm 0.07$—thus the amount of sexual isolation present is not significant). Notice that the coefficient of isolation us-

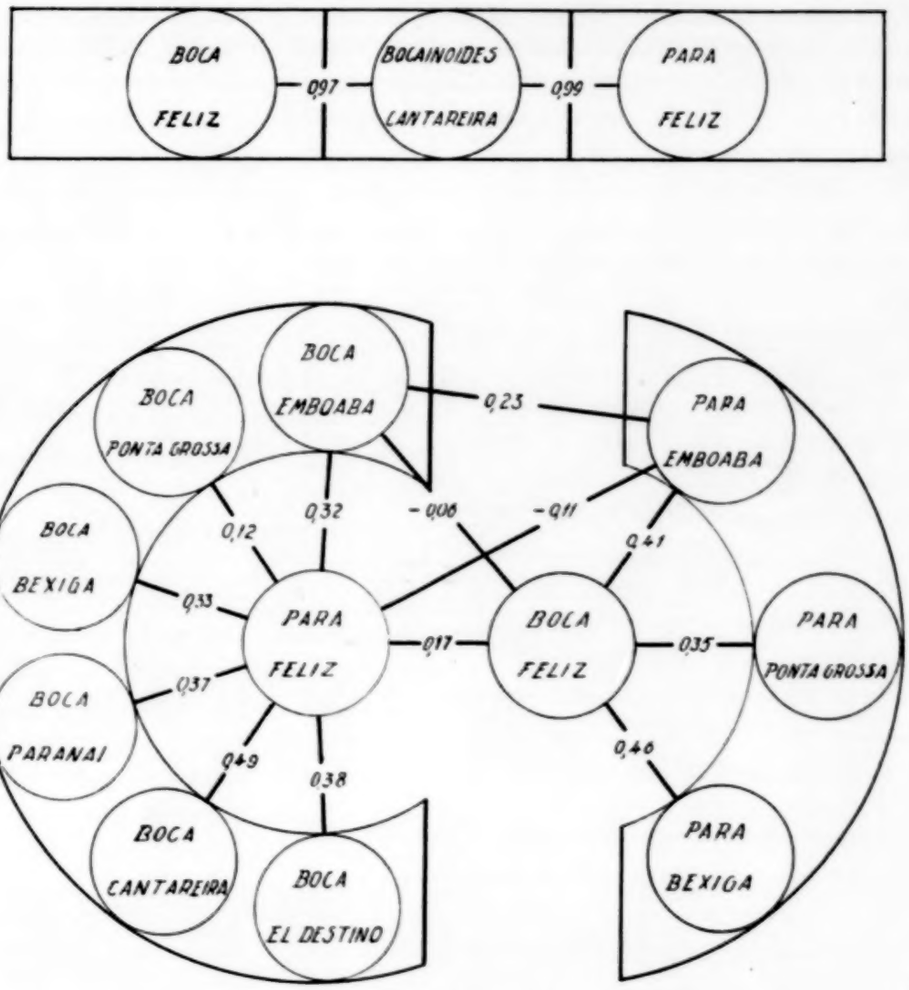


FIG. 1. *Diagram of crosses made for the detection of the quantity of sexual isolation which exist among the three species of the bocainensis subgroup. The numbers refer to the coefficients of joint isolation of Levene* (1949).

ing *bocainensis* males is significant, while that using *parabocainensis* males is not. Comparing now the different coefficients of joint isolation (K 1 and 2) among themselves, it can be seen that only the coefficient obtained in the cross between *D. bocainensis* from Feliz and *D. parabocainensis* from Feliz is significantly different from those obtained in the crosses *D. parabocainensis* from Feliz × *D. bocainensis* from Cantareira and *D. bocainensis* from Feliz × *D. parabocainensis* from Bexiga. If the hypothesis that reproductive isolation is built by natural selection is correct, the isolating mechanisms between related species should, in general, be strongest in those parts of their distribution areas where the danger of hybridization between the species is the greatest. Thus, it is to a certain degree unexpected to find that the coefficient obtained when both species came from Feliz is significantly lower than those calculated for the other two crosses cited. None of the other coefficients of joint isolation varied significantly among themselves.

For the evaluation of the data, some measure of the relative frequency of mating by the two kinds of females is desirable. Table 4 presents, in its extreme righthand column, the coefficients of excess insemination (Levene, 1949), calculated for the different crosses made. This index can serve as a measure of the extent to which the gene flow between the

TABLE 4. *Numbers of females dissected (n) and percentages of those found inseminated (%) in several crosses involving* D. bocainensis, D. parabocainensis *and* D. bocainoides

| Females | | Males | Homogamic | | Heterogamic | | Coefficient of isolation (K 1, 2 and K 2, 1) | Coefficient of joint isolation (K 1 and 2) | Coefficient of excess insemination (m 1, 2) |
|---|---|---|---|---|---|---|---|---|---|
| | | | n | % | n | % | | | |
| Para Feliz | Boca Emboaba | Boca Emboaba | 100 | 72.00 | 101 | 35.64 | 0.49 ± 0.08 | | |
| Para Feliz | Boca Emboaba | Para Feliz | 104 | 60.58 | 99 | 49.49 | 0.15 ± 0.09 | 0.32 ± 0.06 | 0.17 ± 0.06 |
| Para Feliz | Boca P. Grossa | Para Feliz | 97 | 55.67 | 97 | 62.89 | −0.10 ± 0.11 | | |
| Para Feliz | Boca P. Grossa | Boca P. Grossa | 98 | 69.39 | 101 | 43.56 | 0.35 ± 0.10 | 0.12 ± 0.07 | 0.22 ± 0.07 |
| Para Feliz | Boca Bexiga | Para Feliz | 105 | 77.14 | 99 | 27.27 | 0.64 ± 0.07 | | |
| Para Feliz | Boca Bexiga | Boca Bexiga | 104 | 40.38 | 103 | 39.80 | 0.01 ± 0.11 | 0.33 ± 0.06 | 0.32 ± 0.06 |
| Para Feliz | Boca Paranai | Para Feliz | 102 | 84.31 | 95 | 47.37 | 0.48 ± 0.07 | | |
| Para Feliz | Boca Paranai | Boca Paranai | 100 | 62.00 | 98 | 43.88 | 0.25 ± 0.09 | 0.37 ± 0.06 | 0.12 ± 0.06 |
| Para Feliz | Boca Cantareira | Para Feliz | 113 | 77.88 | 98 | 31.63 | 0.60 ± 0.07 | | |
| Para Feliz | Boca Cantareira | Boca Cantareira | 101 | 41.58 | 107 | 21.50 | 0.38 ± 0.11 | 0.49 ± 0.06 | 0.11 ± 0.06 |
| Para Feliz | Boca El Destino | Para Feliz | 102 | 91.18 | 102 | 34.31 | 0.70 ± 0.05 | | |
| Para Feliz | Boca El Destino | Boca El Destino | 107 | 51.40 | 113 | 46.90 | 0.06 ± 0.10 | 0.38 ± 0.05 | 0.32 ± 0.05 |
| Boca Feliz | Para Emboaba | Para Emboaba | 87 | 71.26 | 92 | 39.13 | 0.43 ± 0.09 | | |
| Boca Feliz | Para Emboaba | Boca Feliz | 92 | 64.13 | 90 | 36.67 | 0.38 ± 0.09 | 0.41 ± 0.06 | 0.02 ± 0.06 |
| Boca Feliz | Para Bexiga | Boca Feliz | 102 | 85.29 | 102 | 38.23 | 0.60 ± 0.06 | | |
| Boca Feliz | Para Bexiga | Para Bexiga | 90 | 68.89 | 97 | 44.33 | 0.33 ± 0.09 | 0.46 ± 0.06 | 0.13 ± 0.06 |
| Boca Feliz | Para P. Grossa | Boca Feliz | 101 | 69.31 | 82 | 25.61 | 0.60 ± 0.08 | | |
| Boca Feliz | Para P. Grossa | Para P. Grossa | 62 | 35.48 | 103 | 30.10 | 0.10 ± 0.14 | 0.35 ± 0.08 | 0.24 ± 0.08 |
| Boca Feliz | Para Feliz | Para Feliz | 100 | 72.00 | 101 | 45.54 | 0.35 ± 0.08 | | |
| Boca Feliz | Para Feliz | Boca Feliz | 99 | 57.57 | 102 | 57.84 | −0.004 ± 0.09 | 0.17 ± 0.06 | 0.18 ± 0.06 |
| Boca Emboaba | Para Emboaba | Para Emboaba | 92 | 73.91 | 94 | 48.94 | 0.33 ± 0.09 | | |
| Boca Emboaba | Para Emboaba | Boca Emboaba | 98 | 55.10 | 90 | 46.67 | 0.12 ± 0.10 | 0.23 ± 0.07 | 0.11 ± 0.07 |
| Boca Feliz | Boca Emboaba | Boca Feliz | 101 | 53.47 | 94 | 53.19 | 0.004 ± 0.10 | | |
| Boca Feliz | Boca Emboaba | Boca Emboaba | 99 | 37.37 | 110 | 45.45 | −0.13 ± 0.11 | −0.06 ± 0.07 | 0.07 ± 0.07 |
| Para Feliz | Para Emboaba | Para Emboaba | 96 | 61.46 | 102 | 63.72 | −0.03 ± 0.07 | | |
| Para Feliz | Para Emboaba | Para Feliz | 94 | 50.00 | 91 | 63.74 | −0.19 ± 0.10 | −0.11 ± 0.06 | 0.08 ± 0.06 |
| Bocainoides Cantareira | Para Feliz | Bocainoides Cantareira | 95 | 72.63 | 98 | 1.02 | 0.98 ± 0.01 | | |
| Bocainoides Cantareira | Para Feliz | Para Feliz | 101 | 85.15 | 94 | — | 1.00 — | 0.99 ± 0.01 | 0.01 ± 0.01 |
| Bocainoides Cantareira | Boca Feliz | Bocainoides Cantareira | 102 | 36.27 | 103 | 0.97 | 0.96 ± 0.04 | | |
| Bocainoides Cantareira | Boca Feliz | Boca Feliz | 102 | 65.69 | 106 | 0.94 | 0.98 ± 0.02 | 0.97 ± 0.02 | 0.01 ± 0.02 |

two strains or species studied is in one direction only. As shown there, seven of the fifteen crosses made indicate differences in the mating propensity of the females studied. (However, when the "female mating ratio" coefficient of Merrel (1950) is applied to these data, it shows significant differences in female behavior in the crosses: *D. parabocainensis* from Feliz × *D. bocainensis* from Cantareira ($Mf = 1.37$, $\chi^2 = 8.05$, 1 d. f., $P < 0.01$) and *D. bocainoides* from Cantareira × *D. bocainensis* from Feliz ($Mf = 0.55$, $\chi^2 = 12.02$, 1 d. f., $P < 0.001$), differences not detected when the coefficient of excess insemination is used.) The most extreme cases of differences in female behavior were observed in the crosses *D. parabocainensis* from Feliz × *D. bocainensis* from Bexiga ($m\ 1,2 = 0.32 \pm 0.06$) and *D. parabocainensis* from Feliz × *D. bocainensis* from El Destino ($m\ 1,2 = 0.32 \pm 0.05$). In three crosses the *parabocainensis* females were more active, while in four others the more active were *bocainensis* females. The localities from

which the more active females came were: Feliz (4 cases), Emboaba (1 case) and Ponta Grossa (1 case). In one instance the differential activity occurred between strains of *bocainensis* and *parabocainensis* coming from the same locality (Feliz). On the other hand, the most extreme cases of similarity of behavior were observed in the crosses *D. bocainoides* from Cantareira × *D. parabocainensis* from Feliz ( m1,2 = 0.01 ± 0.01) and *D. bocainoides* from Cantareira × *D. bocainensis* from Feliz (m 1,2 = 0.01 ± 0.02). (Using the "female mating ratio" of Merrel the interpretation of the data will change a little. With this measure the most extreme case of difference in behavior would be present in the cross *D. bocainensis* from Bexiga × *D. parabocainensis* from Feliz, where the Mf is equal to 1.73; and the most extreme case of similarity would occur in the cross *D. bocainensis* from Feliz × *D. parabocainensis* from Emboaba, where the Mf amounts to 1.04.)

## Discussion

In 1950, da Cunha, Burla and Dobzhansky proposed the hypothesis, based on results obtained in *D. willistoni*, that the amount of chromosomal polymorphism found in a population is a function of the number and variety of ecological niches which a population has mastered. Since then, several investigations have been made in order to test the validity of this hypothesis (review in da Cunha, 1955). The most significant results were obtained by da Cunha and Dobzhansky (1954). These authors estimated in quasi-quantitative terms the diversity of ecologic niches accessible to Drosophila that exist in different regions of South America, and verified that these values were positively correlated with the amount of chromosomal polymorphism shown by the populations of *D. willistoni* inhabiting the respective areas. Indeed, these workers were able to use, with generally good results, the estimated ecologic diversity of a particular region to predict the amount of polymorphism to be found in the population occupying it.

As emphasized by da Cunha, Burla and Dobzhansky (l. c.), the assumption that inversions have adaptive properties is essential to their hypothesis. The data obtained in *D. bocainensis* indicate that this is true, at least in part, for the inversions of this species. Thus, although the percentage of heterozygous inversions per individual did not present significant variations in the several regions studied, there was a geographic variation in the frequencies of several gene arrangements. On the other hand, the frequencies observed of inversion 3 – Nn, significantly higher than 50%, proved the heterotic effect of this gene arrangement.

An extension of this theory, to the interspecific level, was proposed by Dobzhansky, Burla and da Cunha (1950). According to them, a more common and widespread species should present a greater quantity of chromosomal polymorphism than other, very closely related to the first, but less common and/or more restricted geographically. The results of da Cunha, Brncic and Salzano (1953) and Salzano (1955), are in agreement with this expectation. The same is true for the data now obtained. *D. bocainensis*, which is the most common and widespread species of the subgroup, has 22 different inversions, while *D. bocainoides* and *D. parabocainensis*, less common and widespread, have only 3 and 2 respectively. Moreover, while the percentage of heterozygous inversions per individual reaches numbers close to 4.00 in *D. bocainensis*, the corresponding numbers in *D. parabocainensis* do not go above 0.41, and it is probable, in spite of the small number of individuals *D. bocainoides* studied, that in this species also this percentage is low.

The analysis of 744 individuals of the bocainensis subgroup from regions where at least two of the species are sympatric (summing up the data obtained in this study and those obtained by Carson), showed that the mechanisms that preserve

them as specific entities are very efficient, since no natural hybrids are found.

In several experiments dealing with sexual isolation in Drosophila the multiple choice technique was employed. Almost all of them were made by the schools of Dobzhansky and Patterson (review in Patterson and Stone, 1952), involving five different groups of species, three belonging to the subgenus Sophophora (saltans, willistoni and obscura) and two to the subgenus Drosophila (virilis and repleta). Our results with the bocainensis subgroup indicate the existence of an incipient sexual isolation between *D. bocainensis* and *D. parabocainensis,* since, in spite of the high percentage of heterogamic crosses, the latter were (with one exception only) significantly fewer than the homogamic ones. It is improbable, however, that the amount of sexual isolation found would, per se, be important in maintaining these forms as distinct species. It is true that the behavior of a species in the laboratory and in nature may be different. But the writer believes that the maintenance of the species of the bocainensis subgroup as discrete entities in nature is due rather to some subtle but efficient ecological barriers that exist between their populations. As emphasized by Blair (1951), reproductive isolation of sympatric species populations by ecological barriers is by no means rare. Indeed, this author was able to demonstrate that at least some such species are capable of hybridization, but do not actually cross in their natural habitats.

*D. bocainoides* is, on the other hand, almost completely isolated sexually from the other two species of the subgroup. The reproductive isolation between this species and its relatives is farther insured by the inviability of the hybrids produced when the sexual isolation is overcome. Neither Carson nor the present writer were able to obtain hybrids in their experiments.

The coefficients of joint sexual isolation obtained in the experiments described above do not show much variability from strain to strain of the same species, even if these strains come from different geographic localities.

## Summary

The bocainensis subgroup of the willistoni group of Drosophila consists of three species. Of these three, *D. bocainensis* is the commonest and most widespread; *D. parabocainensis* is more frequent in localities with cool climates, whereas *D. bocainoides* is characteristic of the super-humid coastal rainforests of São Paulo.

The study of the chromosomal polymorphism showed that in *D. bocainensis*, although it was not possible to find variation in the mean frequency of heterozygous inversions per individual in the several localities tested (all values found were in the neighborhood of 4.00), the frequencies of several gene arrangements presented significant variation between populations of Rio Grande do Sul and São Paulo, and the inversion 3 – Nn, moreover, occurred in frequencies significantly higher than 50%. In *D. parabocainensis* no variation was found in the isolated frequency of the two gene arrangements encountered, nor in the mean frequency of heterozygous inversions per individual, which was very low. Owing to the fact that there is no *D. bocainoides* in natural populations of the state of Rio Grande do Sul, it was not possible to make a detailed study of the chromosomal polymorphism of this species.

The experiments on sexual isolation indicated that the males of *D. bocainensis* and *D. parabocainensis,* even when they can choose between females of their own and of the foreign species, inseminate a high percentage of the latter. In contrast with this, the interspecific crosses involving *D. bocainensis* × *D. bocainoides* and *D. parabocainensis* × *D. bocainoides* presented a very low percentage of insemination. Meanwhile, in spite of the

fact that the frequency of insemination is high in the tests made between *D. bocainensis* and *D. parabocainensis*, almost all of them (with one exception only) showed that a significantly higher percentage of individuals of the same species cross with each other, rather than with individuals of the other species. Figure 1 shows the series of crosses made involving different geographic strains of the species studied. In only two cases significant differences were observed in the coefficients of joint isolation; in these, the cross between *D. bocainensis* from Feliz × *D. parabocainensis* from Feliz indicated a lesser degree of sexual isolation between these populations in relation to that obtained with the crosses *D. parabocainensis* from Feliz × *D. bocainensis* from Cantareira and *D. bocainensis* from Feliz × *D. parabocainensis* from Bexiga.

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# ADAPTIVE CHROMOSOMAL POLYMORPHISM IN AN AUSTRALIAN GRASSHOPPER

M. J. D. White

*Division of Plant Industry, C.S.I.R.O., Canberra, Australia*

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Most of our knowledge of the role played by chromosomal rearrangements in adaptive evolutionary processes has been derived from work on natural and artificial populations of Drosophila, using the salivary gland technique; the studies of Dobzhansky and his associates forming a classical series of investigations in this field. Drosophila possesses many advantages for work of this kind, but also some drawbacks, the chief being that the karyotypes of individuals captured in nature cannot be determined directly, but only by the rather laborious procedure of progeny testing. It is in any case desirable that we should know more about the role of cytological polymorphism in organisms whose systems of population dynamics are different from those found in Drosophila species.

Many, but by no means all, grasshopper species are regularly polymorphic for chromosomal rearrangements which can be studied in the meiotic divisions of the male. Such an examination, carried out on squash preparations, enables one to determine the karyotypes of individuals captured in nature without recourse to progeny testing. In the species dealt with below the making and study of such a preparation takes about 4 minutes, so that up to 100 individuals can be recorded in a day. Thus in studying natural populations one can use considerably larger numbers than when working with Drosophila.

When selecting a species for this type of work it is necessary that it should have chromosomal rearrangements which can be identified with certainty. It is also desirable that it should be available in nature throughout a large part of the year. Both these features are shown by the species dealt with below.

## Distribution, Ecology and Life Cycle of *Moraba scurra*

*Moraba scurra* Rehn (1952) is a slender, wingless insect about an inch long. The endemic Australian genus *Moraba* includes a large number of species (possibly as many as a hundred), several of which are cytologically polymorphic (a cytotaxonomic survey is in progress and will be published later). These insects belong to the family Eumastacidae and are only distantly related to the more familiar grasshoppers of the family Acrididae.

The distribution of *M. scurra* in south eastern Australia (as far as known at present) is shown in figure 1. The region in which it occurs corresponds fairly closely with the "cool temperate area C" on J. Davidson's bioclimatic map of Australia (Andrewartha and Birch, 1954, p. 495). The species is confined to habitats of a special type in which the tall perennial grass *Themeda australis* usually predominates. This, however, is not eaten by the insect, but may be important in other ways (e.g. by providing protection from predators). In captivity *M. scurra* feeds readily on *Helichrysum* spp., which probably constitute its main food in nature, with other Compositae playing a subsidiary role.

Suitable habitats occur in grassland, savannah woodland country and on the ecotones between this and both "dry" and "wet" sclerophyll forest. They were undoubtedly far more widespread before settlement by the white man, but have been largely eliminated or greatly al-

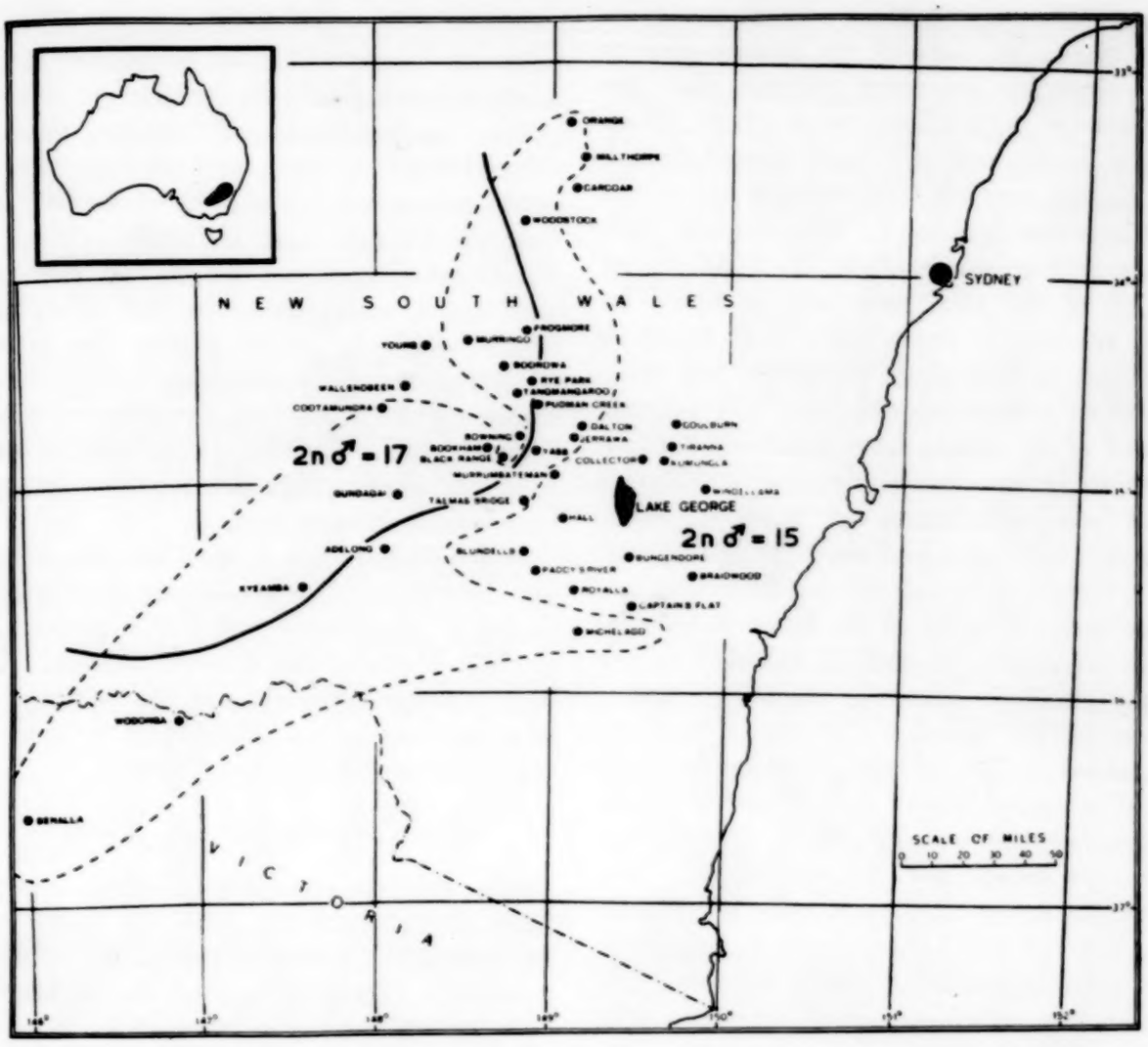


FIG. 1. Map showing the location of the main collecting stations. Sydney and Lake George are only included for purposes of orientation and are not localities for *M. scurra*. The thick line separates the 15- and 17-chromosome populations, while the dashed line encloses an area within which the frequency of the *Standard* CD chromosome exceeds .5 (within this same area the *Tidbinbilla* EF chromosome is absent from most localities). The small inset map of Australia shows, in black, the approximate distribution of *M. scurra*.

tered by close sheep grazing for over 100 years. Thus the colonies of *M. scurra* which still remain occupy relatively minute "islands" in the general area within which the species occurs. Many of these "ecological islands" are the cemeteries of small human communities, i.e. areas of one to several acres which have been fenced for many years to exclude grazing animals, and hence retain much of the native vegetation that has largely disappeared from the heavily grazed land outside. *M. scurra* has been collected from 26 out of 64 cemeteries within its known geographic range (it was not found in the remaining 38 cemeteries examined, some of which had been cleared, cultivated and burned-over). These cemetery populations each consist of a few hundred to a few thousand individuals.

*M. scurra* is a relatively inactive insect with rather feeble locomotory powers which only jumps when provoked and then only for one or two feet. It may consequently be caught by hand quite easily.

Within the known range of the species less than 1% of the total area is occupied

by populations of *M. scurra* at the present time. In view of the limited powers of dispersal we must assume that the cemetery populations were there when these areas were originally fenced (i.e. it is hardly possible that they are the result of later immigration). We conclude that, to a first approximation, $26 \times 100/64$ or 40% of the total area was occupied by *M. scurra* 130 years ago. This figure is subject to two kinds of errors, but these tend to cancel one another: (1) populations of *M. scurra* have probably become extinct in some cemeteries, (2) cemeteries are not distributed at random, since mountain ranges and very "rough" country, which are unsuitable for *M. scurra* are avoided. In spite of the large uncertainties inevitable in such a calculation, we may conclude that the natural distribution of the species 130 years ago resembled a jigsaw puzzle from which a half or two-thirds of the pieces have been removed, but was to a large extent continuous except for the mountains. Today the insect only persists in a few ecological refuges between which migration is quite impossible. Some of these colonies are sufficiently small that we might expect to find evidence of genetic drift having occurred in them.

*M. scurra* is a "winter species." There is only one generation a year. Hatching from the egg takes place in December and January. Most males become adult by May but females overwinter as nymphs and do not become adult until the spring. Copulation has been observed in nature from September 10 to the end of November. Prolificity is low; the maximum number of eggs obtained from a pair mating in captivity was 21.

In all populations of *M. scurra* one finds a variety of color patterns, which are presumably determined genetically. Males may be various shades of gray, brown or buff with stripes or other markings. Females may show all these color patterns but may also be bright green or green with a buff dorsal stripe.

## Methods

Males were collected in nature and studied cytologically in temporary aceto-orcein preparations of entire testes. When desired, such preparations were made permanent by a method similar to that of Conger and Fairchild (1953). First metaphases, on which the scoring was based, occur from the last nymphal instar until the senile phase, i.e. from March through November. In young males the cysts of first metaphases contain 512 cells (White, 1955) but in senile individuals there are fewer cells per cyst—sometimes only 4.

A few individuals in each sample—usually less than 5%—could not be scored, owing to the absence of first metaphases in their testes at the time of fixation. It was possible to determine the karyotype of some (but not many) of these by studying spermatogonial metaphases.

## The Cytology of *M. scurra*

The eastern populations of *M. scurra* have $2n = 15$ in the male (7 pairs of autosomes and a small acrocentric X-chromosome). West of the thick line in figure 1, however, the males have $2n = 17$. Of the seven autosomal pairs present in the eastern race one is a large metacentric with arms of about the same length. We call this the AB chromosome, one of its arms being "A", the other "B". Such a chromosome occurs in many species of Morabine grasshoppers, including the closest relatives of *M. scurra*. In the western populations with $2n = 17$ the AB chromosome has become "dissociated" into two separate acrocentrics (the nature of this "dissociation" will be discussed later).

The second and third pairs of autosomes in order of size will be referred to as the CD and EF elements. Both are heteromorphic as a result of structural rearrangements and give rise to the cytological polymorphism which is the subject of the present study. The overall length of CD is clearly greater than that

of EF, so that the two cannot be confused.

Three types of CD have been identified (fig. 2). Since this chromosome probably arose at a remote period in the phylogeny of the genus by fusion between a "C" and a "D" element we use the name *Standard* to designate a clearly two-armed type of CD with one limb about twice the length of the other. The *Blundell* type of CD is acrocentric, one arm being too minute to be ordinarily detectable; the proximal end of a *Blundell* chromosome

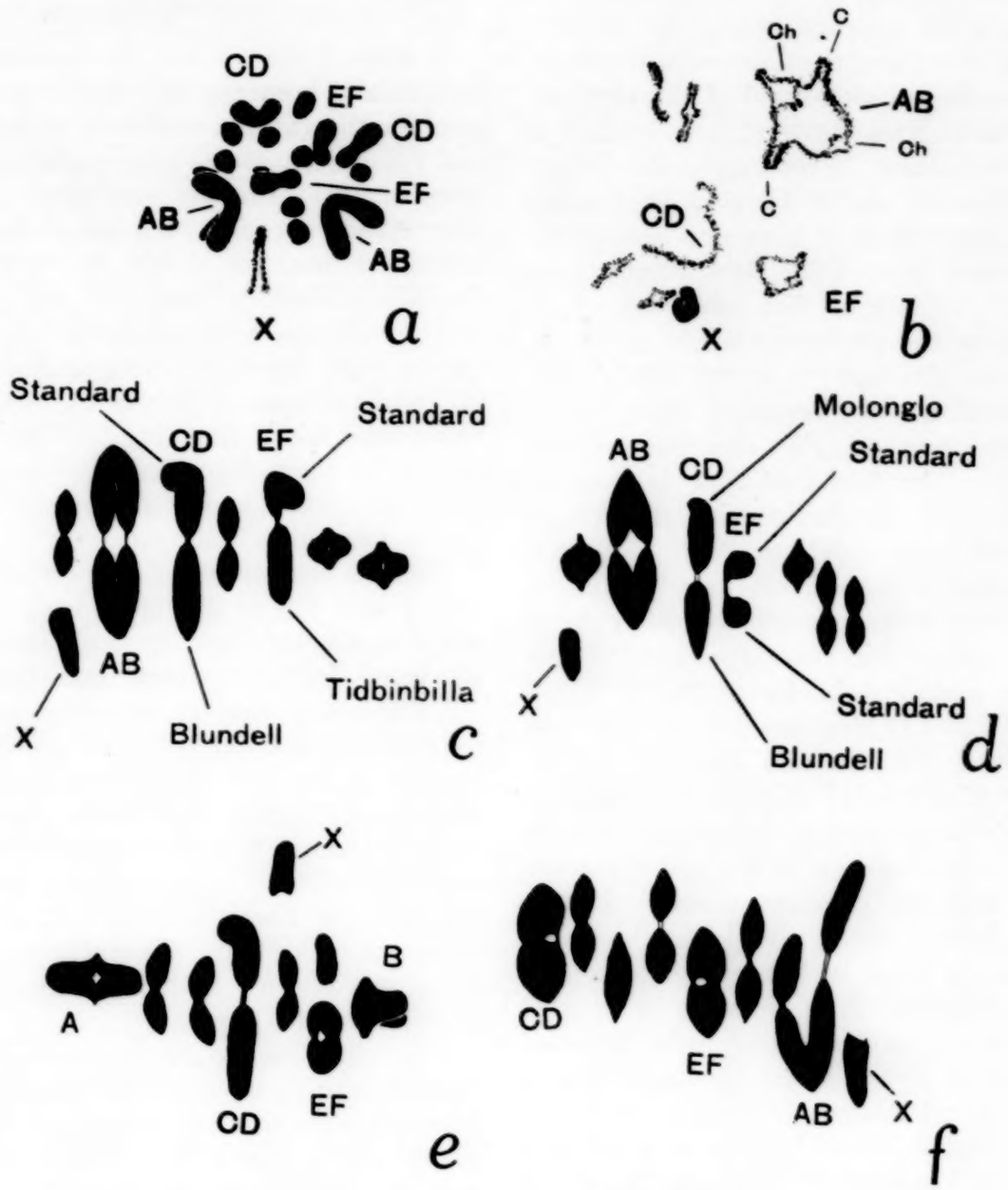


FIG. 2. Cytology of *M. scurra*, showing the principal types of chromosomes encountered. *a*, a spermatogonial metaphase from an individual of the constitution St/St, St/St; *b*, diplotene, showing the positions of the centromeres (c) and the chiasmata (Ch) in the AB bivalent; *c*, first metaphase, in side view, of an individual of the constitution St/Bl, St/Tid; *d*, first metaphase of an individual from the Bungendore locality of the constitution Mol/Bl, St/St (*a*, *b*, *c* and *d* are all from the 15-chromosome race); *e*, first metaphase from an individual of the 17-chromosome race of the constitution St/Bl, St/St; *f*, first metaphase from an individual from Paddy's River, heterozygous for a "broken" AB chromosome (this individual St/St, St/St). In *d* the EF bivalent has a single chiasma in its shorter arm, in *e* and *f* the EF bivalents have chiasmata in both arms.

looks sharply pointed at first metaphase. A third type of CD designated *Molonglo* (these are local geographical names) has only been found with certainty in one population (Bungendore) but it or a similar one seems to occur in one other locality (Taemas Bridge). A *Molonglo* CD chromosome appears nearly acrocentric, but the short arm is of appreciable length, so that the proximal end of the chromosome looks truncate or slightly hooked at first metaphase. Presumably the *Standard, Blundell* and *Molonglo* CD chromosomes were derived from one another by pericentric inversion. But there is no critical evidence on this point and we do not know the phylogeny of the three sequences, although it seems likely that *Standard* was the ancestral one.

Two types of EF chromosome are known. The *Standard* type is a metacentric with one arm considerably longer than the other, while the *Tidbinbilla* EF chromosome is an acrocentric. *Standard* and *Tidbinbilla* presumably differ by a single pericentric rearrangement.

The meiotic behavior of St/St, St/Bl and Bl/Bl CD bivalents has already been described (White and Morley, 1955). In St/Bl bivalents chiasma formation is entirely suppressed in the region between the two centromeres, so that there is never more than one chiasma, which is invariably distal. St/St and Bl/Bl bivalents frequently have both a proximal and a distal chiasma. The situation in Bl/Mol bivalents is similar to that in St/Bl ones, i.e. except in the rarest instances only a single distal chiasma is formed. It is not known what would happen in a St/Mol bivalent since such bivalents have not been seen with certainty. Mol/Mol bivalents frequently form a chiasma in the short arm, a fact which helps in distinguishing Mol/Mol from Bl/Bl individuals.

Chiasma formation in St/St, St/Tid and Tid/Tid EF bivalents follows the same general rules as in the case of the CD chromosome. In St/Tid bivalents the chiasma is always between the short arm of the *Standard* chromosome and the distal end of the *Tidbinbilla* one.

In addition to the AB, CD and EF pairs of autosomes there are four pairs of small acrocentric autosomes which do not ordinarily show any polymorphism.

## The Natural Populations

In table 1 are set out the numbers of individuals homozygous and heterozygous for the various sequences of the CD and EF chromosomes encountered in 48 samples (46 different localities). The geographical location of most of the collecting stations is shown in figure 1. Paddy's River "A" and "B" are about half a mile apart, Windellama "A" and "B" a mile apart, Komungla "A" and "B" two miles apart, Dalton "A" and "B" half a mile apart, Bowning "A" and "B" four miles apart, Rye Park "A" and "B" two miles apart and Boorowa "A" and "B" a mile and a half apart.

There is one sample of 777, one of 700, one of 400, five of 200 and forty smaller samples ranging down to single individuals from Pudman Creek and Orange. All the larger samples represent several collections made on different dates, but in view of the very low mortality in the adult stage (until the senile phase is reached) summation of such collections is clearly justified. The spring and autumn collections at Paddy's River "A" (which represent different generations) and those at Collector (which do not) are, however, treated separately.

The chromosome frequencies in the various samples may readily be calculated from the data in table 1 and are shown graphically in figure 3. It will be seen that the frequency of *Blundell* ranges from zero to about 0.9, while that of *Tidbinbilla* ranges from zero to about 0.3.

We can conclude little from the very small samples. Three populations (Boorowa "A", Wodonga and Benalla—all cemetery populations) appear to be monomorphic for the *Standard* types of both chromosomes. No colonies monomorphic for *Blundell* or *Tidbinbilla* have been

TABLE 1. *Observed numbers of homozygotes and heterozygotes in adult male samples*
(All collections except the first were made in 1955)

| | Chromosome CD | | | Chromosome EF | | | |
|---|---|---|---|---|---|---|---|
| | St/St | St/Bl | Bl/Bl | St/St | St/Tid | Tid/Tid | N |
| *2n = 15 populations* | | | | | | | |
| Paddy's River "A" Oct.–Nov. 1954 | 12 | 30 | 23 | 23 | 38 | 4 | 65 |
| Paddy's River "A" Apr.–May | 13 | 54 | 34 | 57 | 40 | 4 | 101 |
| Paddy's River "B" Mar.–Apr. | 40 | 105 | 55 | 121 | 73 | 6 | 200 |
| Blundells Apr. | 11 | 29 | 12 | 52 | — | — | 52 |
| Hall* July–Oct. | 74 | 345 | 358 | 558 | 207 | 12 | 777 |
| Bungendore Apr.–May | 12† | 79‡ | 109 | 193 | 7 | — | 200 |
| Royalla Aug.–Sept. | 70 | 313 | 317 | 393 | 278 | 29 | 700 |
| Michelago* Aug.–Nov. | 279 | 115 | 6 | 390 | 10 | — | 400 |
| Captain's Flat* Sept. | 3 | 21 | 27 | 36 | 12 | 3 | 51 |
| Braidwood* Sept. | 1 | 1 | 1 | 3 | — | — | 3 |
| Windellama "A"* Apr. | 3 | 15 | 6 | 17 | 6 | 1 | 24 |
| Windellama "B" Apr.–May | 7 | 23 | 22 | 35 | 14 | 3 | 52 |
| Komungla "A"* May | — | 4 | 22 | 23 | 3 | — | 26 |
| Komungla "B" May–June | 16 | 90 | 72 | 157 | 21 | — | 178 |
| Tiranna May | 1 | 8 | 8 | 17 | — | — | 17 |
| Goulburn June | 19 | 75 | 71 | 132 | 32 | 1 | 165 |
| Collector April | 2 | 37 | 161 | 105 | 74 | 21 | 200 |
| Collector Oct.–Nov. | — | 26 | 174 | 101 | 85 | 14 | 200 |
| Taemas Bridge Aug.–Sept. | 21§ | 18§ | 3 | 42 | — | — | 42 |
| Murrumbateman* July–Aug. | 26 | 106 | 68 | 166 | 31 | 3 | 200 |
| Yass* July | 4 | 17 | 3 | 19 | 5 | — | 24 |
| Jerrawa July | 2 | 2 | 1 | 5 | — | — | 5 |
| Dalton "A"* July | 3 | 1 | 1 | 4 | 1 | — | 5 |
| Dalton "B" June | 6 | 3 | — | 9 | — | — | 9 |
| Pudman Creek June | — | 1 | — | 1 | — | — | 1 |
| Woodstock* July | 9 | 3 | — | 12 | — | — | 12 |
| Carcoar* July | — | 2 | 12 | 8 | 3 | 3 | 14 |
| Millthorpe* July | 1 | 4 | 1 | 4 | 2 | — | 6 |
| Orange* Oct. | 1 | — | — | 1 | — | — | 1 |
| Adelong* Aug. | 10 | 1 | — | 9 | 2 | — | 11 |
| Wodonga* Aug. | 22 | — | — | 22 | — | — | 22 |
| Benalla* Aug. | 17 | — | — | 17 | — | — | 17 |
| *2n = 17 populations* | | | | | | | |
| Black Range July | 1 | 1 | 3 | 4 | 1 | — | 5 |
| Bookham* July | 6 | 14 | 2 | 22 | — | — | 22 |
| Bowning "A" July | — | 18 | 36 | 43 | 10 | 1 | 54 |
| Bowning "B" July | 2 | 3 | 2 | 4 | 3 | — | 7 |
| Tangmangaroo July | 6 | 4 | 1 | 11 | — | — | 11 |
| Rye Park "A" July | 5 | 11 | 5 | 21 | — | — | 21 |
| Rye Park "B" July | — | 2 | 1 | 3 | — | — | 3 |
| Boorowa "A"* July | 60 | — | — | 60 | — | — | 60 |
| Boorowa "B" June–July | 10 | 28 | 6 | 44 | — | — | 44 |
| Frogmore* July | 3 | — | — | 3 | — | — | 3 |
| Murringo* May–June | 79 | 25 | — | 104 | — | — | 104 |
| Young* June | 8 | 31 | 23 | 57 | 5 | — | 62 |
| Wallendbeen* Aug. | — | 10 | 12 | 17 | 4 | 1 | 22 |
| Cootamundra* Aug. | 1 | 3 | — | 4 | — | — | 4 |
| Gundagai* Aug. | 10 | 5 | 1 | 16 | — | — | 16 |
| Kyeamba Aug. | 4 | 4 | 1 | 6 | 3 | — | 9 |
| | | | | | | | 4227 |

* Cemetery populations. † Mol/Mol not St/St. ‡ Mol/Bl not St/Bl.
§ Some CD chromosomes in this population classified as Blundell were probably Molonglo or a similar rearrangement.

found. In the case of Boorowa "A" we suspect that genetic drift has produced the monomorphism, since at a point a mile and a half away (Boorowa "B") a population exists which contains *Standard* and *Blundell* CD chromosomes in approximately equal numbers and which shows more than 50% heterozygotes (in a sample of 44 individuals). The monomorphic Boorowa Cemetery population probably consisted of several hundred individuals in 1955, but almost certainly less than 1000. It is entirely possible that this colony arose from very few pairs of individuals which became isolated when the cemetery was established and the surrounding country began to be intensively grazed. It is also quite likely that accidental or deliberately-caused grass fires in the cemetery may have reduced the *M. scurra* population to very small numbers on one or more occasions in the past.

In the case of the Wodonga and Benalla populations the evidence is less clear. These are peripheral populations and it is not known whether any cytologically polymorphic colonies occur in the same general region. It is hence entirely possible that this whole area was occupied by a cytologically monomorphic "race" of *M. scurra* 130 years ago. But the alternative hypothesis that the Wodonga and Benalla cemetery populations have become homozygous as a result of genetic drift cannot be excluded at present.

At the Bungendore locality the CD chromosome is represented by the *Blundell* and *Molonglo* sequences, but *Standard* is absent, this being the only population in which it is lacking altogether. Presumably *Molonglo* has replaced *Standard* at this locality owing to some kind of incompatibility between them. If these two sequences are related as overlapping pericentric inversions so that each differs from *Blundell* by a single inversion, crossovers in the region of overlap may lead to the production of gametes with duplications and deficiencies by St/Mol heterozygotes. But at the Taemas Bridge locality all three sequences probably coexist. This population was in a rather senile condition when studied, and it was not easy to distinguish the *Molonglo* chromosomes from *Blundell* ones, or to be certain that they were *Molonglo* rather than a fourth sequence different from St, Bl, and Mol. Provisionally, all non-*Standard* CD chromosomes at the Taemas Bridge locality have been classified as *Blundell* for statistical purposes.

Except for the Boorowa "A", Wodonga and Benalla localities, all populations from which samples of over five individuals were obtained show polymorphism for the CD chromosome, but only 25 of the 46 localities are known to show polymorphism for the EF pair. And in the case of CD we have a complete range from populations in which Bl/Bl individuals greatly outnumber St/St ones to colonies in which the reverse is the case; while in the case of EF, Tid/Tid homozygotes are always a small minority.

Certain geographic regularities in the frequencies of the various sequences will become apparent from a comparison of figures 1 and 3. In figure 1 a dotted line encloses an area within which the frequency of *Standard* CD chromosomes exceeds that of *Blundell* ones, whereas elsewhere the relation is reversed. It will be observed that this area is bisected by the line separating the 15- and 17-chromosome "races," i.e. there is a similarly high frequency of *Standard* CD chromosomes on either side of the line. Within the same area the *Tidbinbilla* sequence seems to be generally absent, only the Dalton "A" and Kyeamba populations being exceptional in this respect.

Although most of the western populations have a high frequency of *Standard* CD chromosomes and lack the *Tidbinbilla* sequence, neither statement is true of an area which includes Young, Wallendbeen and the two Bowning localities. Another area in which the cytological composition of the populations seems to be rather uniform includes the two Komungla colonies, Tiranna and possibly Goulburn.

By way of contrast to these regulari-

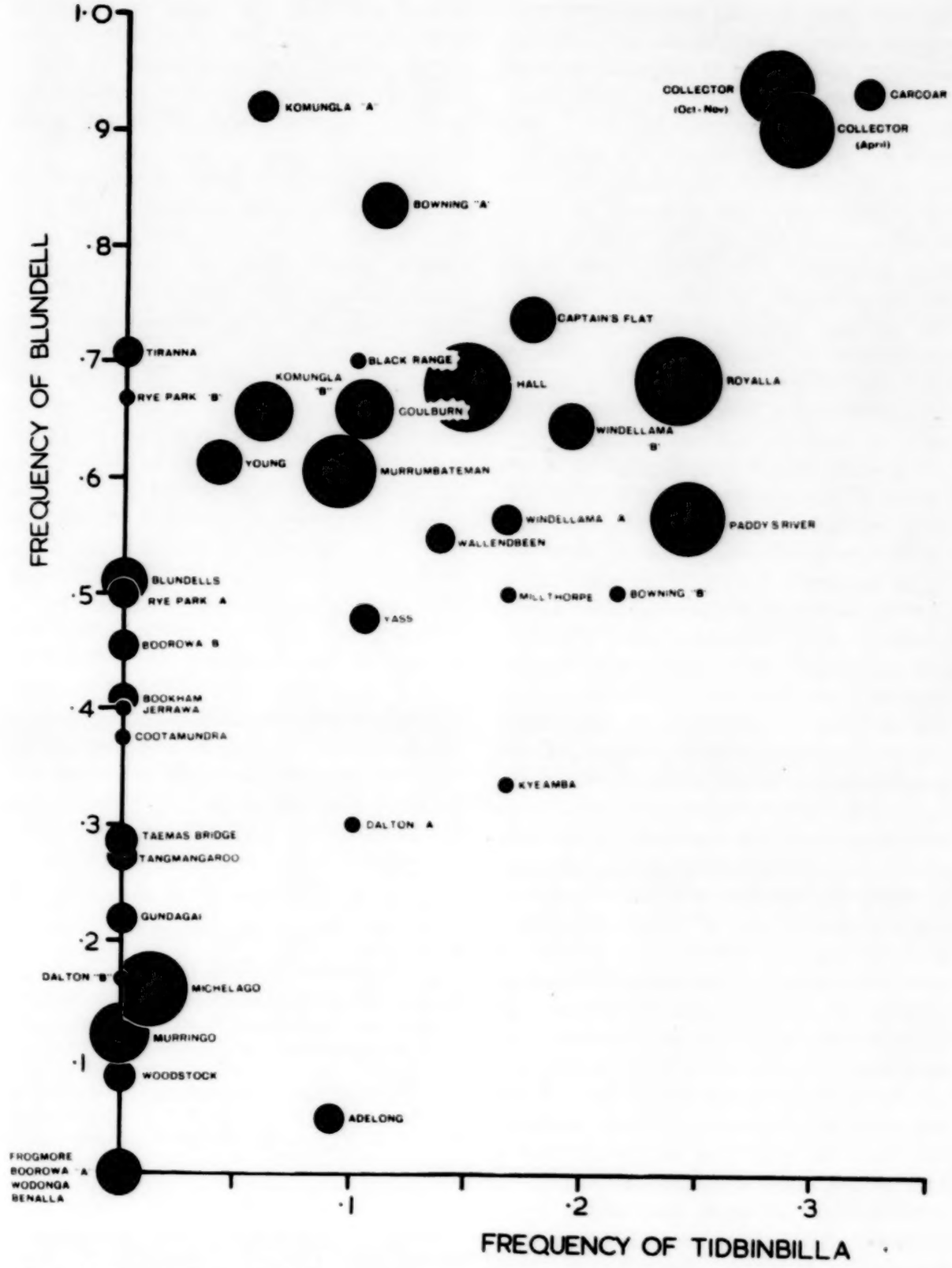


FIG. 3. Relation between the frequencies of the *Blundell* sequence of the CD chromosome and the *Tidbinbilla* sequence of the EF chromosome in 41 different localities. The five sizes of black circles represent samples of different sizes. In this diagram the samples from Paddy's River A and B have been combined. The Bungendore population, which is anomalous in lacking the *Standard* CD chromosome, which is replaced by *Molonglo*, has been omitted from this diagram.

ties, some very striking irregularities may be pointed out. Woodstock and Carcoar (22 miles apart) are at opposite ends of the frequency graph (fig. 3). The samples from these localities are small and hence not very significant, but the colonies at Royalla and Michelago, only 14 miles apart, are quite different in cytological composition on the basis of very large samples. The Young and Murringo populations, 15 miles apart, are also very unlike. These irregularities in the distribution of chromosome frequencies could not be correlated with any differences of elevation, rainfall or type of vegetation between the various localities.

The data shown graphically in figure 3 suggest that a correlation may exist between the frequencies of the *Blundell* and *Tidbinbilla* gene arrangements, there being a tendency for samples showing a high frequency of *Blundell* to also show a relatively high frequency of *Tidbinbilla* and conversely. The situation is complicated by the fact that over large geographic areas *Tidbinbilla* is apparently absent altogether. Also, many of the samples are too small for the chromosomal frequencies to be determined with sufficient accuracy. On the basis of the samples of over 20 individuals, using an angular transformation, $r = .68$ which, for 22 degrees of freedom, is highly significant. However, if we consider the samples of over 100 (omitting Murringo, where *Tidbinbilla* is absent) the correlation, although still significant at the 5% level, is determined almost entirely by the samples from Michelago and Collector. Thus, although a correlation probably does exist, the evidence for it is not conclusive, and in any case its significance remains uncertain (a genuine correlation would probably point to some type of genetic interaction between the two systems of chromosomal polymorphism).

## The Evidence for a Heterotic Effect on Male Viability

Assuming panmixia, it is possible to determine from data such as those of table 1 whether differential mortality of homozygotes and heterozygotes has occurred prior to the adult stage, by calculating the deviations from expectation on the basis of the Hardy-Weinberg equilibrium.

It is uncertain whether populations of *M. scurra* are strictly panmictic. On general grounds it seems unlikely that individuals select mates of one karyotype rather than another. However, some genotypes may be more sexually active or prolific than others. And the vagility of individuals of this species is so low that even in an area of one or two acres the density of the population is such that mating between close relatives is likely to occur more often than would be the case if motility produced complete randomization. Such a tendency would produce departures from the Hardy-Weinberg equilibrium in the direction of an excess of homozygotes and a corresponding deficiency of heterozygotes.

The most satisfactory method for comparing the frequencies of homozygotes and heterozygotes with those expected on the basis of complete panmixia and equal viability is that due to Levene (1949) used by Dobzhansky and Levene (1948) and

TABLE 2. *Levene test on whole data*

*Chromosome CD*

(42 samples, totalling 4123 individuals)

| | |
|---|---|
| Sum of 31 negative deviations | − 92.03478 |
| Sum of 10 positive deviations (1 sample showed no deviation) | + 9.23636 |
| | − 82.79842 |
| | $\sigma^2 = 667.01827$ |
| | $t = -3.20592$ |
| | $P = .0007$ |

*Chromosome EF*

(27 samples, totalling 3758 individuals)

| | |
|---|---|
| Sum of 17 negative deviations | − 58.16173 |
| Sum of 8 positive deviations (2 samples showed no deviation) | + 22.71959 |
| | − 35.44214 |
| | $\sigma^2 = 289.16927$ |
| | $t = -2.08422$ |
| | $P = .0186$ |

Epling, Mitchell and Mattoni (1953). In table 2 we give the results of the application of this method to our data (negative deviations indicate a deficiency of homozygotes, positive deviations an excess). With the present material it is not necessary to employ the correction for misclassification needed in the case of Drosophila. For chromosome CD there is significant evidence of a heterotic effect on male viability. The samples with negative deviations greatly outnumber those showing positive deviations, all those of over 100 individuals show negative deviations and the $t$ value for the data as a whole gives $P = .0007$.[1]

However, although the heterotic effect seems undoubtedly real, it is a relatively slight one and none of the deviations for the individual samples is significant by itself. Dobzhansky and Levene (1948) have used the ratio $\Sigma(h - H)/\Sigma H$ as a measure of the overall deviation from the Hardy-Weinberg equilibrium. For their data on *Drosophila pseudoobscura* this ratio was equal to $-0.147$, i.e. there was a 14.7% deficiency of homozygotes. On the other hand, Epling Mitchell and Mattoni (1953) could find no consistent deficiency of homozygotes in this same species. In the case of the CD chromosome of *M. scurra* the ratio only amounts to $-0.0329$, i.e. the average deficiency of homozygotes was 3.29%.

In the case of the EF chromosome the evidence for a heterotic effect is much less strong, the $t$ value giving significance at the 2% level but not at the 1%. Again, there are more samples with negative deviations than with positive ones, but three of the samples of over 100 (Komungla B, the April sample from Collector and Murrumbateman) show positive deviations. In fact, without the sample of 700 from Royalla (for which $h - H = -22.45746$, $\sigma^2 = 93.12318$, $t = -2.327$) there would be no real evidence for any heterotic effect on male viability in the case of the EF chromosome. However, the total evidence does point to a slight heterotic effect, although weaker and less consistent than in the case of the CD chromosome. For the EF $\Sigma(h - H)/\Sigma H = -0.0128$, i.e. there is only a 1% deficiency of homozygotes on the whole of the data, although the Royalla population does show a 5% deficiency.

The most obvious interpretation of the "missing" homozygotes is that they are actually dead, i.e. that there has been a selective mortality between the time the egg is laid and the adult stage. An alternative explanation might exist if the actual collection of the samples was non-random. If homozygotes were less active than heterozygotes they might be missed by the collector, particularly in long grass. In an attempt to test this possibility in an indirect way, all the later samples were placed in a lucite plastic tube 2 inches in diameter, subdivided into five sections 4½ inches long by partitions each containing 31 ¼ inch holes. The apparatus was set up vertically and the insects were placed in batches (usually 20 to a batch and never more than 25) in the bottom chamber, and allowed to climb up the sides and through the holes in the partitions until approximately 10% of the sample had reached the top chamber.

[1] Dr. Bruce Wallace has pointed out to me (*in litt.*) that the Levene test will give an apparent deficiency of homozygotes whenever the viability of the heterozygotes exceeds the geometric mean of the viabilities of the two homozygous classes. Thus, under certain circumstances, a significant negative value for $t$ may be due, not to heterosis, but to the heterozygotes having an intermediate viability. The latter situation would not be likely to be associated with balanced polymorphism (unless viability were negatively correlated with some other component of the adaptive value such as fecundity), but would in most cases lead to a rapid elimination of one type of chromosome from the population. In the present instance it is clear on general grounds that we are dealing with chromosomal polymorphisms which are a permanent feature of most of the populations and not a transient phenomenon destined to disappear in a few generations. Thus the apparent deficiency of homozygotes is almost certainly genuine and the conclusion that we are dealing with a heterotic effect justified.

When this was so the chambers were cut off from one another by sliding partitions and the insects from each chamber removed for cytological study. In order to have the conditions of illumination reasonably uniform the whole apparatus was enclosed in a sleeve of black paper and illuminated from above by a 100 Watt lamp.

Thus each sample brought in from the wild, after removal of any individuals lacking a hind leg or otherwise injured, was fractionated into 5 sub-samples, supposedly ranging from the most active to the least active individuals. The result of this phase of the work was, however, entirely negative, i.e. the statistical analysis revealed no significant difference between the karyotypic composition of the sub-samples obtained in this manner. Thus there is no support for the view that cytological heterozygosity or homozygosity has any direct effect on activity, at any rate under the admittedly artificial conditions of the experiment. Thus it seems likely that collecting is essentially random as far as the karyotypic constitution of the individuals is concerned and that the "missing" homozygotes are, in fact, dead. The selective mortality probably operates during the egg stage or in the early nymphal instars, because the deficiency of homozygotes in the natural populations does not seem to increase from April to October.

Although there is no evidence for an effect of homo- or heterozygosity on general activity, it remains possible that there might be a specific effect on sexual activity. During September–November the males caught *in coitu* in the Royalla, Hall, Collector and Michelago populations were recorded separately. A chi square test does not reveal any significant difference between the composition of the "mating samples" and the general population, but the numbers were hardly large enough (117 mating individuals altogether) for this purpose.

### Cytologically Aberrant Individuals

It is not surprising that in the course of examining 4227 individuals some cytologically aberrant ones should have been encountered. The first metaphase karyotypes of some of these are shown in figure 2, *f* and figure 4. One type of aberration that has been found in six individuals (two from Paddy's River "B", two from Komungla "B", one from Royalla and one from Michelago) is a "broken AB" in the heterozygous condition. Such individuals show, at meiosis, a trivalent composed of the normal AB chromosome paired with two acrocentrics (fig. 2, *f*). This trivalent is almost always "lopsided," with one acrocentric higher than the other. Such individuals could represent the remnants of a former condition in which the population was regularly polymorphic for a broken versus fused AB. Alternatively, it is possible that the AB undergoes fragmentation in its centromere region rather readily, and that "broken AB's" are repeatedly arising within the 15-chromosome race, so that one or two in a thousand individuals carry a recently-arisen break.

Obviously, both the acrocentrics arising in this way must possess a centromere if they are to persist. The "lopsided" appearance of the trivalent suggests that the centromere of one of the acrocentrics may be less efficient than that of the other. It is uncertain whether these "broken AB's" arise by simple breakage through the centromere itself, between the components of a compound or double centromere or by a translocation in which the freshly broken ends are "capped" (a term due to Muller and Herskowitz, 1954) with chromosomal material derived from one of the other elements. The transmission of the acrocentrics derived by fragmentation of the AB seems to be entirely regular in these six individuals, both at the premeiotic divisions and at meiosis, i.e. the trivalent is invariably present at first

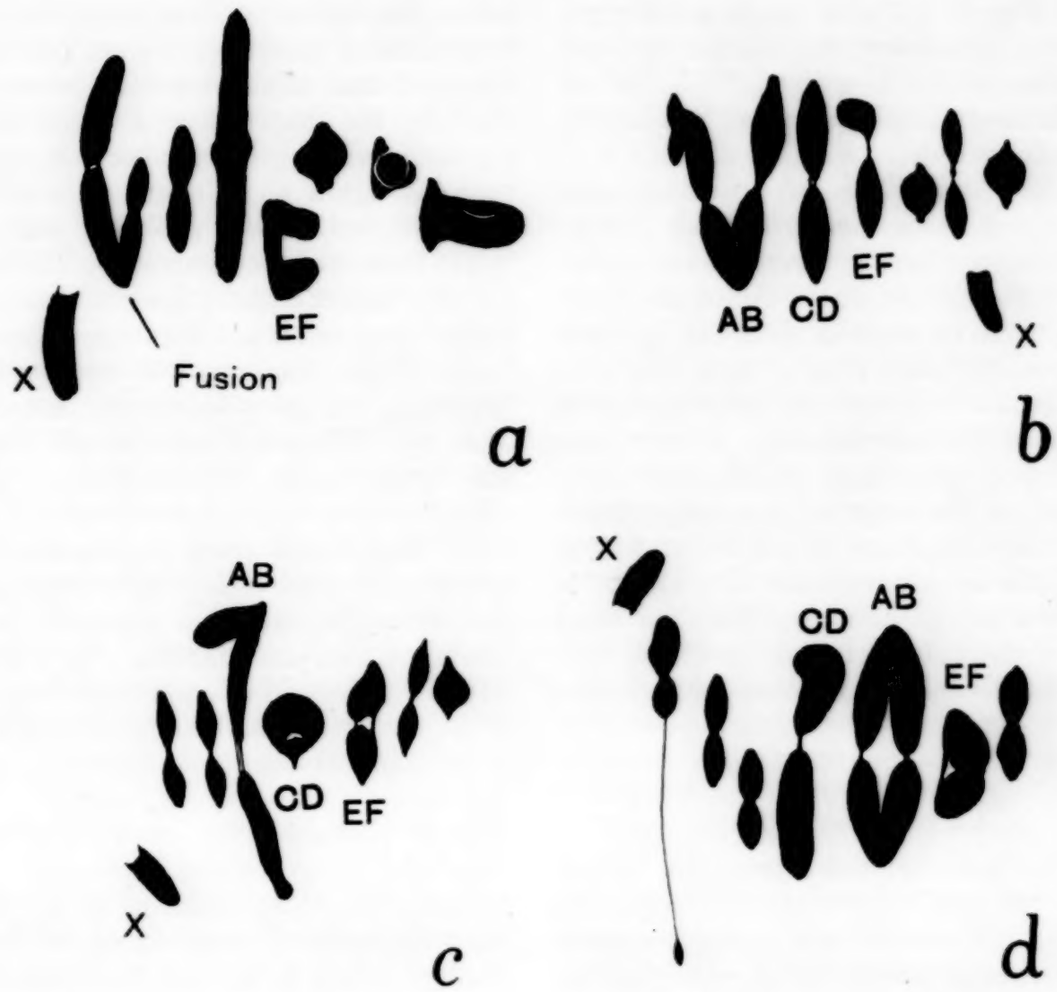


FIG. 4. First metaphases, in side view, of various cytologically aberrant individuals. *a*, from Young, heterozygous for a centric fusion; *b*, from Hall, heterozygous for a "broken AB" and some kind of translocation involving one of the small autosomal pairs; *c*, another individual from Hall which had a group of first metaphases with a large deletion in one of the AB chromosomes; *d*, an individual from Paddy's River B, heterozygous for a "weak place" in one of the small bivalents (the "weak place" greatly stretched on the spindle).

metaphase, and in spite of its asymmetrical appearance it disjoins quite regularly.

Additional evidence that breakage occurs rather readily in the middle region of the AB chromosome is provided by one individual from the Hall population which had most of one arm of one of its AB chromosomes deleted in some (but not all) the cells of the testis (fig. 4, *c*). Another individual from Hall (fig. 4, *b*) had some kind of translocation which involved a break in one of its AB chromosomes; in this instance the condition was systemic, i.e. present in all cells. This individual showed, at first metaphase, a trivalent consisting of the unbroken AB and two apparently acrocentric elements, to the centric end of one of which one of the four small bivalents was regularly attached. The exact constitution of this individual is not clear, but it was probably heterozygous for a translocation involving a break in one member of the smallest chromosome pair and a break in an AB chromosome close to the centromere; it may have carried two normal small chromosomes in addition (i.e. it may have been trisomic for this element).

An individual heterozygous for a centric fusion was found in the Young popu-

lation (fig. 4, *a*). One of the small chromosomes was fused with a larger element, but whether the latter was "A", "B" or CD is uncertain, since these are almost the same length.

A few individuals were encountered that were heterozygous for "weak places" which become greatly stretched and pulled out on the spindle at the first meiotic division. An example is shown in figure 4, *d*, but such "weak places" have also been seen in the AB and EF chromosomes; whenever encountered they were present in all first metaphases of the individual. In spite of the enormous extension which they undergo there is no evidence that these "weak places" are actually liable to break at cell division. Similar "weak places" have been found in a few individuals of some other species of Morabine grasshoppers.

## Significance of the 15- and 17-Chromosome Races

It is clear that the races with "fused" and "broken" AB chromosomes are rightly included within a single species. They occupy distinct areas which are apparently contiguous for a distance of about 150 miles. The two forms have the same rearrangements in their CD and EF chromosomes and carry them in similar frequencies on either side of the interracial boundary (fig. 1). Crossing experiments between the two races have been successful, i.e. hybrid offspring have been obtained from a number of pairmatings (some of these will be studied cytologically when older).

If we are correct in believing that the southern tableland of New South Wales was formerly occupied by a semi-continuous population of *M. scurra*, covering at least a third of the total area, it follows that some "mixed" colonies must have existed along the boundary, as a result of migration. In spite of much searching by the author and Mr. L. J. Chinnick, no such colonies have been found. Nevertheless, some may yet exist and be found later. However, the fact that none have been discovered so far suggests that broken/fused heterozygotes are not heterotic and that mixed colonies, when isolated by the destruction of much of the habitat under grazing, become monomorphic again as a result of selection. The situation is thus probably quite different from that encountered by Wahrman (1954) in the mantid *Ameles heldreichi*, where most or all colonies are apparently "mixed" (in this case the broken/fused heterozygotes are presumably heterotic). It is also different from that met with in the grasshopper *Trimerotropis sparsa* (White, 1951) where two "mixed" colonies were found along the boundary between a 21- and a 23-chromosome race; and from the situation reported in the mollusc *Purpura lapillus* by Staiger (1954) where broken/fused heterozygotes occur in habitats ecologically intermediate between those inhabited by the cytologically homozygous types.

It is probable that in *M. scurra* the fused AB preceded the broken AB condition. The closest relative of *M. scurra* is an undescribed species from the Hunter Valley, which is in some respects morphologically intermediate between *scurra* and species of the genus *Keyacris*. It (and they) all possess a "fused" AB. Thus it seems likely that at some time in the past the broken AB condition managed to establish itself in the western part of the range of *scurra*. The absence of "mixed" colonies at the present time (apart from the occasional occurrence of heterozygotes at a few localities within the range of the 15-chromosome race) argues against broken/fused heterozygotes being heterotic and suggests that the initial establishment of the "broken" condition may have been due to drift rather than to selection.

## General Discussion

In work on the North American grasshoppers belonging to the genera *Trimerotropis* and *Circotettix* (White 1951, 1954) it was found that if a species was characterized by cytological polymorphism at

all, every colony showed some degree of polymorphism, i.e. no chromosomally monomorphic populations of such species as *Trimerotropis sparsa, T. gracilis, T. suffusa, T. cyaneipennis* and *C. rabula* are known.

In the case of *M. scurra,* on the other hand, chromosomally monomorphic colonies do exist, although it must remain an open question for the present whether they are the result of human interference with the habitat during the past 130 years. The finding of these colonies does, however, indicate that *M. scurra* is less dependent on its cytological polymorphism than the above mentioned species. All the monomorphic colonies of *scurra* found were of the same type, namely St/St, St/St, and it is not known whether any monomorphic colonies homozygous for *Blundell* exist (it seems most unlikely that a colony homozygous for *Tidbinbilla* could persist).

Although our data provide some information on the viability of males of various genetic constitutions, they do not permit one to calculate the adaptive values of the karyotypes. The viability of males is only one component of the adaptive value of a genotype (Levene, Pavlovsky and Dobzhansky, 1954), the viability, longevity, degree of sexual activity and fecundity of both sexes being all involved in determining the total adaptive value. While it is likely on general grounds that in most species selective values in the two sexes are rather strongly correlated, Levitan (1951, 1954) has presented evidence for selective differences between males and females of *Drosophila robusta* carrying various gene arrangements in the X and second chromosomes.

In *M. scurra* the evidence on male viability in the case of the CD chromosome points unmistakably to a heterotic effect. Thus unless there is a negatively heterotic effect on the other components of the adaptive value (which seems highly unlikely) we may conclude that the St/Bl polymorphism owes its preservation (except at Boorowa, Wodonga and Benalla cemeteries) to an adaptive superiority of the St/Bl karyotype over both St/St and Bl/Bl. Presumably the hierarchy of adaptive values is St/Bl > St/St > Bl/Bl within the area enclosed by a dotted line in figure 1, but St/Bl > Bl/Bl > St/St outside this area.

In the case of the EF chromosome the evidence is less certain. The low frequency of *Tidbinbilla,* in all populations in which it occurs (.01 to .32), suggests that Tid/Tid individuals have a low adaptive value in all environments, a conclusion strengthened by the relatively large deficiencies in this class when the observed numbers are compared with those expected on the basis of the Hardy-Weinberg equilibrium. But as far as male viability is concerned, the evidence for a true heterotic effect, in the case of the EF chromosome, is rather weak. There may, of course, be a more significant heterotic effect in the female; alternatively it is possible that *Tidbinbilla* may be retained in some populations as a result of some kind of interaction with the heterotic mechanism associated with the CD chromosome, rather than on account of any heterotic effect of its own.

The low frequency of *Tidbinbilla* in all localities where it exists at all seems to imply that the genetic properties of *Tidbinbilla* chromosomes are, in general, similar throughout the entire area known to be inhabited by *M. scurra* and consequently (bearing in mind what we have said about the restricted dispersal powers of the insect) that they have remained rather constant over tens of thousands of generations (i.e. years).

In the case of chromosome CD, on the other hand, it is clear that there are some populations in which Bl/Bl homozygotes have a higher adaptive value than St/St ones and others where the situation is reversed. Only transplantation experiments, which would take several years to complete, would decide whether environmental differences or differences in the genetic properties of *Standard* and *Blundell* chromosomes at the various lo-

calities play the major role in determining these relationships.

In a population containing the *Standard* CD, *Blundell* CD *Standard EF* and *Tidbinbilla EF* chromosomes there will be nine genotypes which can be arranged in a 3 × 3 table. Assuming panmixia, it is possible to test by a $\chi^2$ procedure for interaction between the CD and EF chromosome pairs in determining male viability. Such a test was applied to the eleven samples of over 100 individuals, but the result was inconclusive, i.e. there was no convincing evidence of interaction, since none of the eleven $\chi^2$ values is significant at the 5% level.

By comparison with Drosophila populations, those of *M. scurra* are probably very stable, both in size and genetic composition. The fact that the species has only one generation a year means that successive generations do not encounter such different environments as those provided by seasonal changes in the case of temperate (and some tropical) species of Drosophila. And the fecundity and mobility of *M. scurra* are both sufficiently low to preclude the kind of violent fluctuations in population size which seem to be common in Drosophila. It is in the light of such a stable system of population dynamics (at least prior to the catastrophic effect of grazing during the past 130 years) that we may seek to understand the role of adaptive karyotypic polymorphism in this species of insect. The slightness of the heterotic effects should not cause surprise, and is certainly not a reason for refusing to recognize the adaptive nature of the cytological polymorphisms of *M. scurra*. The samples were taken from natural environments, in which we would expect the deficiencies of homozygotes to be much less than they would be under unusual or artificial conditions. Adaptive polymorphisms which have been perfected by thousands of generations of selection are likely to be homeostatic to a high degree—i.e. we must expect the heterotic effects to be minimal under average environmental conditions, increasing as the environment departs more and more from the mean.

But no amount of homeostatic buffering will preserve a species under conditions of catastrophic change of the environment in unprecedented ways. If present trends continue, the future of *M. scurra* would appear to be extremely problematical. More and more colonies may become monomorphic as a result of drift, as the Boorowa cemetery one appears to have done already. But it seems quite likely that the species as a whole faces extinction within the next century, as its habitats are destroyed, one by one, either temporarily or permanently. Its genetic system no doubt adapted it to the temporal and spatial fluctuations of the environment before the coming of the pastoral industry, but seems inadequate to cope with the widespread environmental deterioration which is the result of grazing.

## Summary

*Moraba scurra*, a grasshopper of the tablelands of southeastern Australia, has two races, one with 2n = 15 in the male, the other with 2n = 17. The difference in chromosome number is apparently due to the dissociation of a large metacentric chromosome, AB, which occurs in the 15-chromosome populations, into two acrocentric elements, A and B, in the 17-chromosome populations. Hybrids between the two races have been obtained without difficulty in the laboratory, but have not yet been studied cytologically.

Both races are polymorphic for the same structural rearrangements (probably pericentric inversions) in two different chromosome pairs, CD and EF. In the case of the CD chromosome there is a slight but significant deficiency of homozygotes among the adult males, when the observed numbers are compared with those expected on the basis of the Hardy-Weinberg law. The corresponding deficiency in the case of the EF chromosome is small and of doubtful significance.

Altogether, 4227 male individuals from 46 localities have been studied. 24 of these localities are cemeteries, which represent "ecological refuges" where the vegetation is protected from the effects of grazing by sheep. In three of these cemeteries cytologically monomorphic populations occur; at least one of these populations probably owes its present composition to the operation of genetic drift during the past 130 years. Apart from these cytologically monomorphic populations, almost all colonies of the species show polymorphism for chromosome CD, but many are monomorphic for chromosome EF.

In addition to the widespread rearrangements, there are some which are possibly confined to single colonies or small areas and others which have only been encountered in single individuals.

## Acknowledgments

Throughout the course of this work many useful suggestions were received from Dr. K. H. L. Key, of the Entomology Division, C.S.I.R.O., whose critical judgment has been of great assistance. Mr. L. J. Chinnick of the same division, gave invaluable aid with the field collecting and himself discovered a number of the colonies studied. Help in collecting the insects was also kindly provided by Drs. F. H. W. Morley, Bruce Griffing, D. L. Hayman and J. Langridge, Mr. C. Davern, Mrs. Helen Morley, Mrs. M. Parker and members of the author's family. Advice and help with the statistical treatment of the data was also generously provided by Drs. Griffing and Morley, who devoted much time to testing hypotheses of genetic interaction between the CD and EF chromosome pairs.

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# A BIOMETRIC STUDY OF THE EVOLUTION OF FISSIPED CARNIVORES [1]

M. Crusafont-Pairó and J. Truyols-Santonja

*Museo Municipal de Sabadell, Sabadell, Spain*

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## Introduction

The incidental proposal of two angular measurements, made by us on the most representative teeth of fissiped carnivores, suggested to us the systematic observation of these values in various species of each family. This systematization became increasingly demanding and led us to undertake a search for a relationship between the two measurements and for a graphic representation of that relationship. On placing the values in a scatter diagram on a system of coordinates, we clearly observed the real biometric significance of the points graphed.

Examination of the placing of these points provided us with objective data on the systematic positions of the various groups of carnivores and on their phylogeny, in such a way as to permit comparison of the graphic representation with ideas previously expressed by zoologists and paleontologists. The almost perfect agreement resulting from the two different approaches has impelled us to explain our method, which is the aim of the present note.[2]

## The Angles $\alpha$ and $\beta$

The measurements in question are two angles observed on the carnassial teeth of fissiped carnivores.

The angle designated as $\alpha$, taken on the lower carnassial ($M_1$), measures a relationship between the height of the protoconid and the length of the talonid. It is obtained as follows: On an orthogonal projection of the labial side of the tooth two lines are drawn, one tangential to the two external convexities of the base of the crown, above the beginning of the roots, and the other tangential to the tip of the protoconid and the highest point of the talonid (which generally is the tip of the hypoconid). (See fig. 1.)

Values observed in the various species of carnivores studied vary from 4° to 105°, thus covering a wide range within which are included the *arctoid* forms, with low values (ursids, procyonids, canids, and mustelids), and the *aeluroids*, with higher values (viverrids, hyaenids, and felids). (See table 1.) The boundary

Table 1. *Extreme values of angle* $\alpha$

| | |
|---|---|
| Ursidae | 6.3°– 31° |
| Canidae | 21.5°– 49° |
| Mustelidae | 4° – 72° |
| Viverridae | 34° – 55° |
| Hyaenidae | 48° – 83° |
| Felidae | 55° –105° |

between the two groups is established at about 45°, just where are found those forms (*Cynodictis*, etc.) considered by previous authors as the most primitive of the fissipeds. (See fig. 2.) This value should, then, be considered as primitive (synthetotypical) and as a point of departure for the whole array of later carnivores. The distribution of particular forms demonstrates that the most specialized types, in one direction or another, are at the extremes of the wide range under consideration while the forms that are primitive, chronologically or morphologically speaking, are in the neighborhood of the original type. The angle $\alpha$ on milk

[1] This article is a translation from the Spanish manuscript. The translation has been authorized and approved by the authors. Editor.

[2] In a work published in Spain, in which we established one of the measurements here under discussion, attention was drawn to the possibility of developing a new biometric discipline which might be called "masterometry" (Crusafont-Pairó and Truyols-Santonja, 1953).

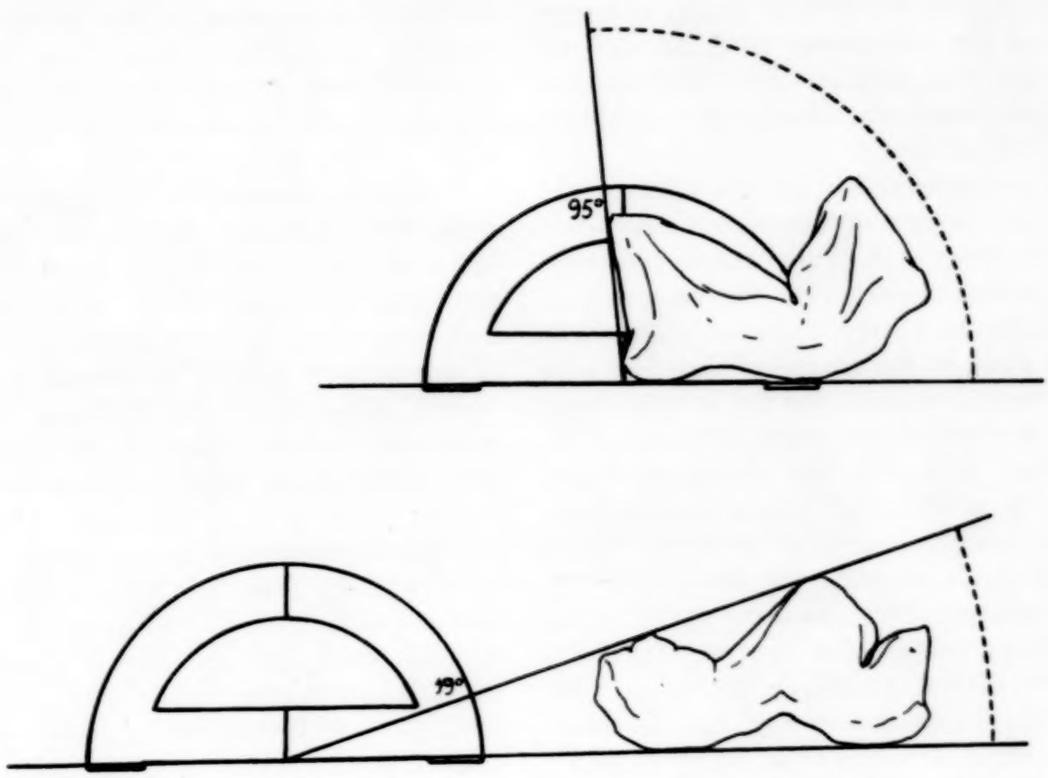


FIG. 1. Measurement of the angle $\alpha$. Above, the lower carnassial of a hypercarnivore. Below, that of a hypocarnivore.

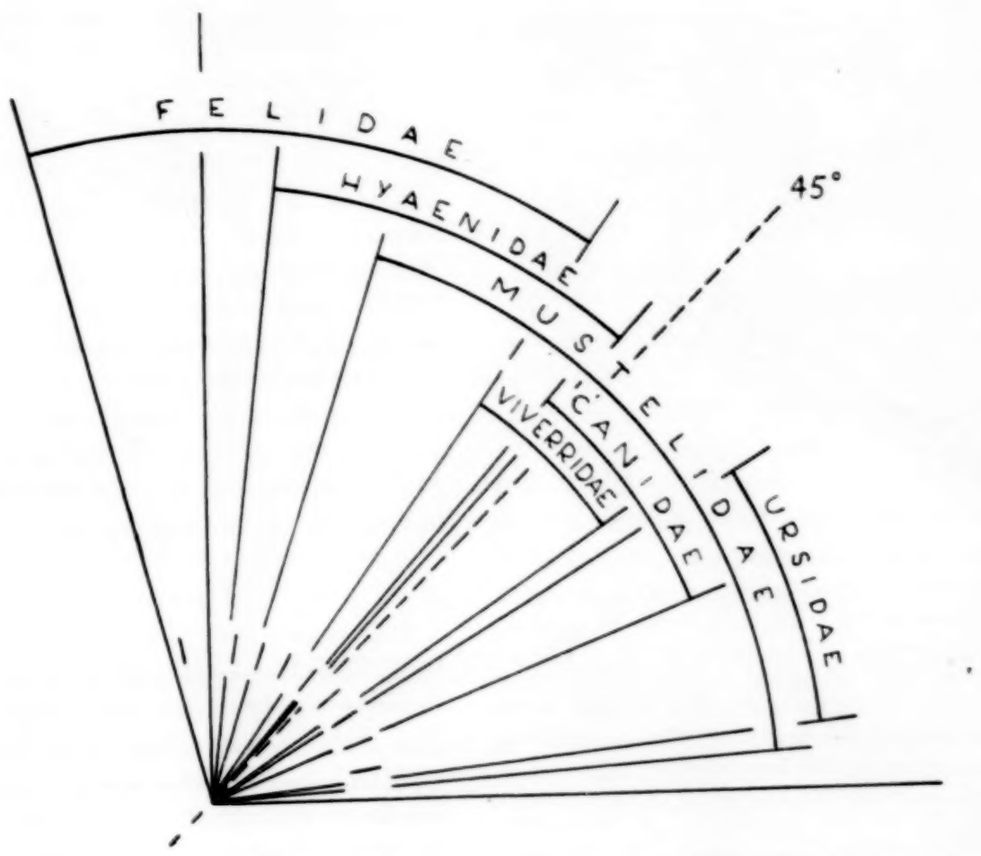


FIG. 2. Range of variation of the angle $\alpha$ for the several families (see table 1).

teeth ($D_4$) of the arctoid group is larger than on the permanent teeth and in the aeluroids it is smaller. In both instances the milk teeth are nearer the synthetotypical condition.

Departing from the central value of 45° there has been progressive differentiation in both directions, giving rise to the present polymorphism of the carnivores. Achievement of the extreme values has taken place in the course of time and in a symmetrical way around the synthetotypical value, which has acted as a sort of directional axis for the whole complex. Analysis of different faunal associations, carried out separately by localities, shows that in each instance the mean value of $\alpha$ varies around 45°, as if the radial variation were subject throughout to the influence of the primitive direction. St. Gérand, Aquitanian in age, has 38 carnivores whose $\alpha$ varies from 32.5° to 68.5°, mean 43.5°. Winterhof-West, Burdigalian, has 26 carnivores, between 20° and 68.5°, mean 40.4°. The Vindobonian complex of Vallés-Penedés has 20, between 7° and 78°, mean 43.5°. Recent Europe has 17, between 6° and 90°, mean 43.9°. (See fig. 4.)

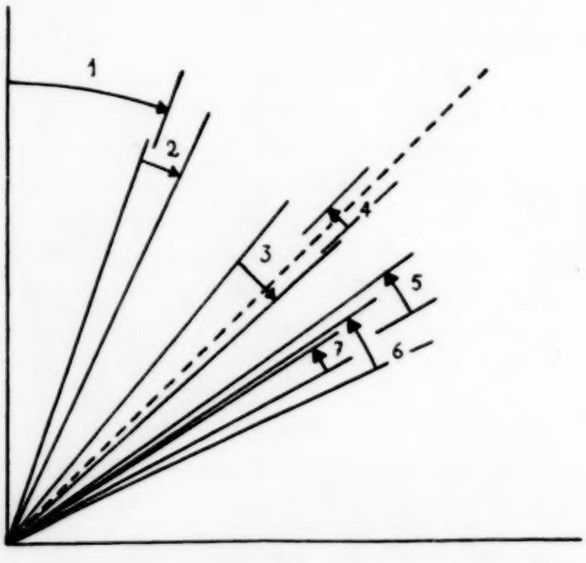


FIG. 3. Values of the angle $\alpha$ in some deciduous lower carnassials of various species of fissipeds compared with that angle in the permanent carnassial of the same species. The arrows point from the value for the permanent to that for the deciduous tooth. Note that in the hypercarnivores the angle decreases, while the opposite occurs in the hypocarnivores. 1. *Felis tigris*. 2. *Grivasmilus jourdani*. 3. *Semigenetta elegans*. 4. *Martes laevidens*. 5. *Amphicyon schlosseri*. 6. *Broiliana nobilis*. 7. *Laphyctis* (?) *vorax*.

The angle designated as $\beta$ measures a relationship between the maximum length and width at the level of the protocone on the upper carnassial ($P^4$). It is obtained as follows: on an orthogonal projection of the occlusal surface of the carnassial a line is drawn from the metacone to the most anterior projection of the parastyle and another from the metacone to the protocone. (See fig. 5.) The values obtained for this measurement have a range somewhat greater than the first octant of a circle, from about 10° to about 55°. In contrast to $\alpha$, here the arctoid group has the higher values, while the aeluroids tend to be in the region of lower values. (See table 2.) The bisecting axis of the complex, which thus corresponds with the angle of the primitive (synthetotypical) forms, is 22.5°, precisely half the value synthetotypical for $\alpha$. (See fig. 6.) These relationships underline the significance of the new measurement which, as for $\alpha$, places the primitive forms in a central part of the range and the specialized forms at both extremes, although the direction of divergence for the groups in question is here reversed.

TABLE 2. *Extreme values of angle* $\beta$

| | |
|---|---|
| Ursidae | 26° –52° |
| Canidae | 15° –36° |
| Mustelidae | 19° –43.5° |
| Viverridae | 18° –25° |
| Hyaenidae | 13.6°–21.5° |
| Felidae | 10° –25° |

## THE RELATIONSHIP BETWEEN $\alpha$ AND $\beta$

The preceding exposition demonstrates that there is a true and strict relationship between the two measurements. The fact that progressive increase in one is accompanied by likewise progressive decrease in the other suggests the presence of some degree of correlation between them. In spite of the fact that our data do

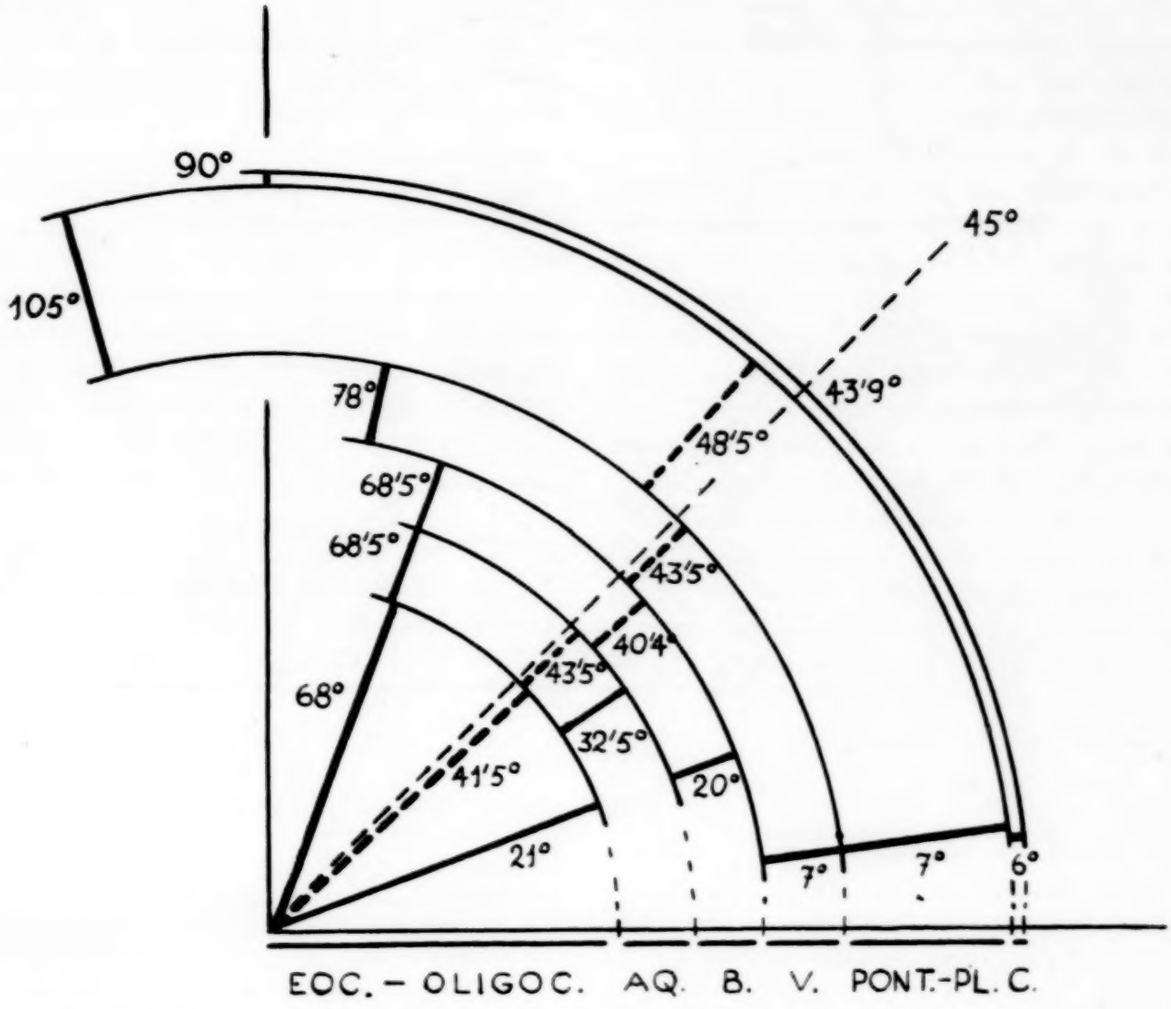


FIG. 4. Ranges and means of the angle $\alpha$ in various faunal associations of different ages. Eoc.-Oligoc., Eocene-Oligocene. Aq., Aquitanian. B., Burdigalian. V., Vindobonian. Pont.-Pl., Pontian-Pliocene. C., Pleistocene-Recent.

not really relate to a geographic population or to members of a single phyletic lineage, we have employed the usual method for study of correlation in order to see the kind of relationship between the two characters. We may justify taking this liberty by the fact that in the progressive morphological differentiation of the carnassials from the primitive type all forms can be thought of as derived from such a common progenitor, in accordance with what we know of evolution in this group. In this way, the diverse species may be considered simply as variants of the same type, setting aside the ideas of time and space and equating the whole complex, for purposes of calculation, with a single population.

The number of species examined is 197 (13 ursids, 4 procyonids, 55 canids, 61 mustelids, 13 viverrids, 15 hyaenids, and 36 felids). Following the short method of Simpson and Roe, we have made a correlation table of corresponding values of $\alpha$ and $\beta$. Pearson's coefficient of correlation, calculated in this way, is $-0.643$. It is evident that there is a strong negative correlation between the variates compared.

The graph of points corresponding with each pair of values on Cartesian coordinates shows that they fall into a band symmetrically arranged around a hypothetical line which represents the trend of the complex. This is the regression line for this relationship, and it has noteworthy

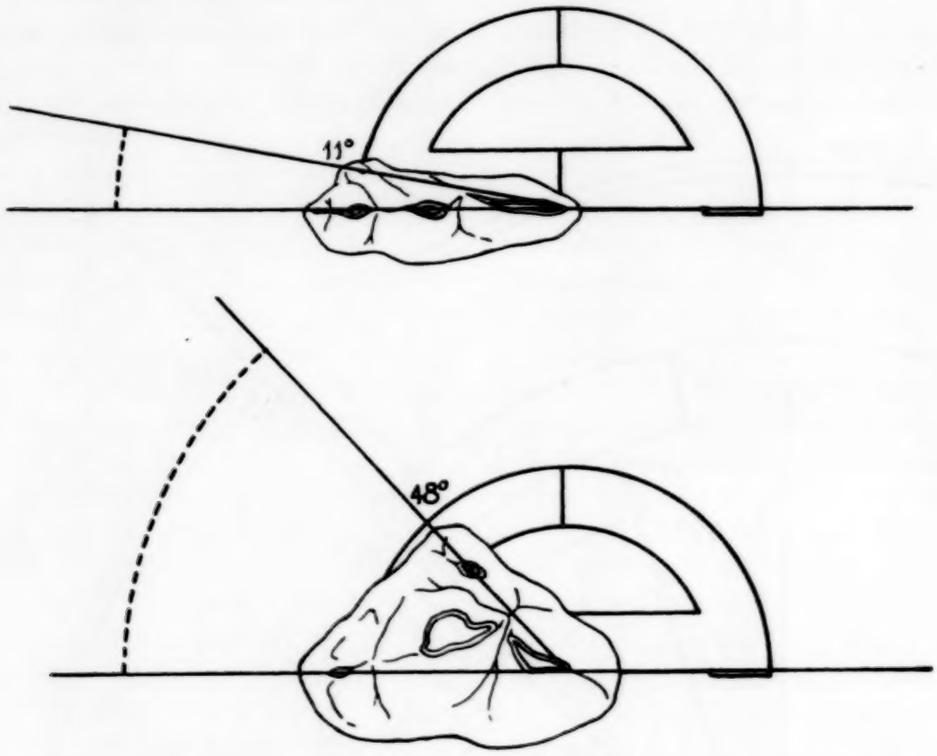


FIG. 5. Measurement of the angle $\beta$. Above, the upper carnassial of a hypercarnivore. Below, that of a hypocarnivore.

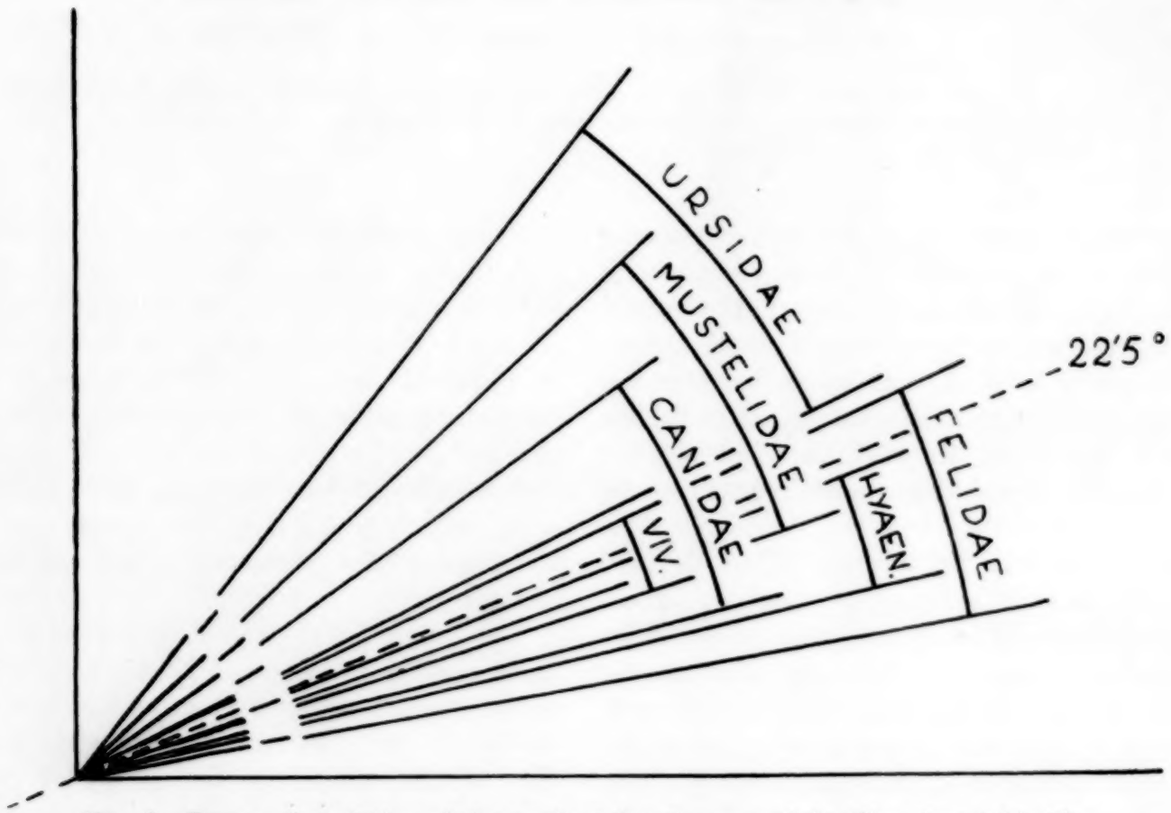


FIG. 6. Range of variation of the angle $\beta$ for the several families (see table 2).

biological significance, as will appear in what follows. (See fig. 7.)[3]

The equation for this line represents the kind of connection that exists between the two variates. If the ratio of the two were equal throughout, this would doubtless be a segment of an equilateral hyperbola. That is not the case, and since a graph on logarithmic coordinates brings the curve into a straight line, the equation must correspond with a polytropic curve, that is, with a hyperbola of higher order. Calculation of that curve yields the following:

$$y = 137.898x^{-0.52048}$$

which in practice may be rounded to

$$y = 126x^{-0.5} \text{ or } y = \frac{126}{\sqrt{x}}.$$

Within the inevitable margin of error, this is the equation that represents approximately the ideal curve or fitted line toward which the compiled values tend. We shall call this curve the *canonical line*.

Close examination of the position of each individual point yields considerable information about the meaning of the dispersion observed within the constellation of values. It stands out clearly that temporal and systematic-evolutionary factors have been in play in a basic way. We can, indeed, deduce the following from observation of the whole distribution:

a. The synthetotype and its immediate neighbors, constituting the basic zone of the fissipeds, lie just on the calculated curve and around its central part.

b. To the right of the synthetotype and along the whole width of the band are situated the hypercarnivores (the *aeluroid branch* of the curve), while to the left are similarly the hypocarnivores (*arctoid branch*). The various families occur in an overlapping way along the graph, in accordance with their greater or lesser degrees of specialization: viverrids, hyaenids, and felids on the aeluroid branch, and canids, mustelids, procyonids, and ursids on the arctoid branch. (See fig. 8.)

c. Within each family there is a logical and rational distribution of each and all of

[3] The scale used in the diagram is based on the tangents of the angular values, because that is the most significant representation of the variability of this function. Furthermore the values entered are tangents of $\alpha/2$ and $\beta/2$ in order to avoid excessively high values of the tangents for angles near 90° and the jump to $\pm \infty$ that occurs on crossing that threshold.

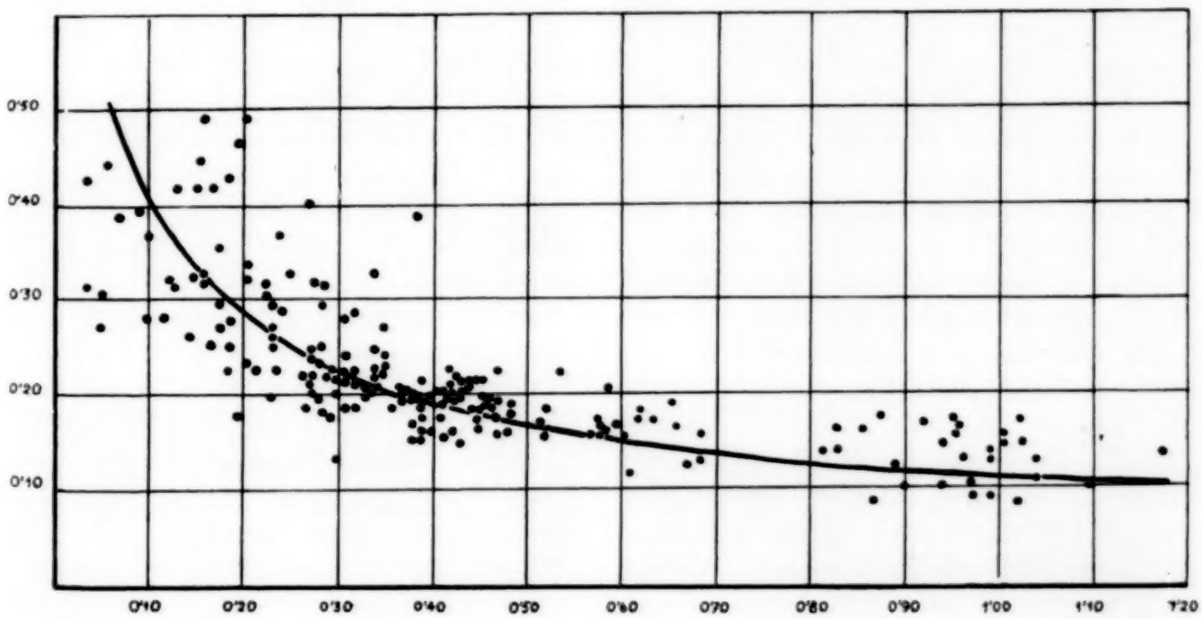


FIG. 7. Scatter diagram of points corresponding to the relationship of tan $\alpha/2$ and tan $\beta/2$, and calculated curve.

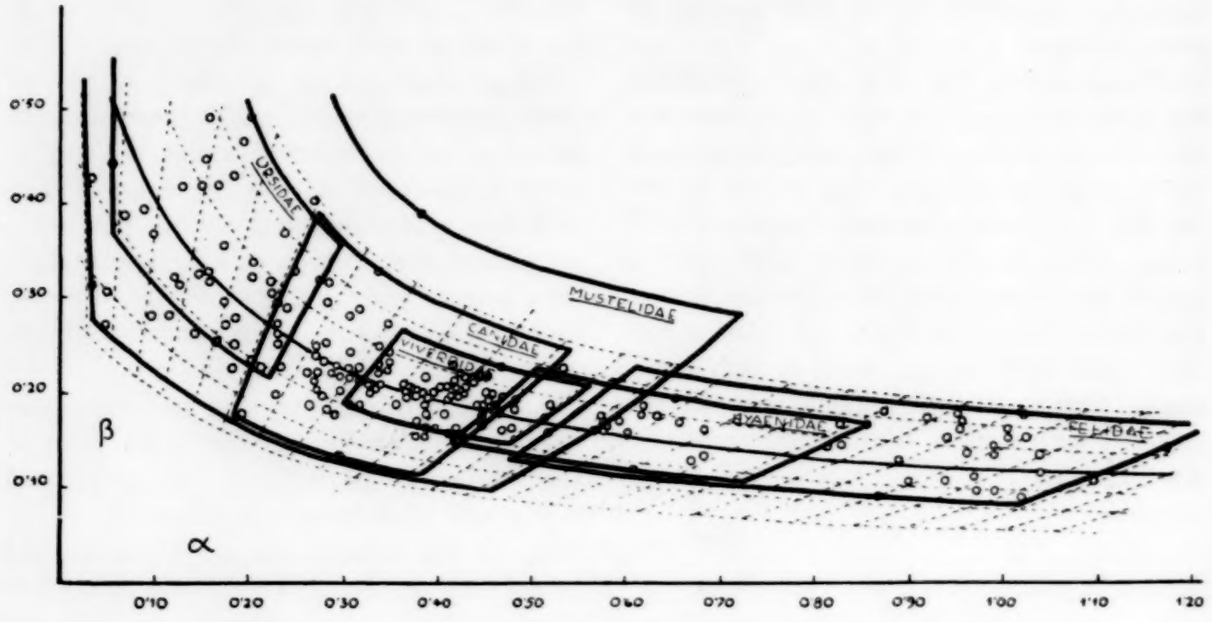


FIG. 8. Distribution on the graph (as in fig. 7) of the families of fissiped carnivores.

the forms in accordance with their morphological and temporal specialization. The primitive types of each family are nearest the curve (the canonical line), while the specialized types are generally apart from it and even near the limits of the zone.

The point of departure of this complex thus corresponds with the coordinates 0.414 and 0.198 (representing respectively the angles 45° and 22.5°). Precisely in the immediate vicinity of this theoretical point are found the various species of the Eocene carnivore *Cynodictis,* recognized by students as situated near the base of the fissipeds and near their origin from the miacids in the creodont complex. The two great ecological categories, the hypo- and hypercarnivores, are found with some degree of inevitable overlapping in each of the two branches of the curve, in such a way that the most specialized forms are found at the ends of that curve. On the other hand the most primitive families (canids, viverrids) are so situated on the graph as to form an area surrounding that of *Cynodictis* and related genera of the basal block of the complex. Within each family the primitive forms are, almost without exception, quite near the calculated curve and the specialized forms occupy niches at some distance from the respective norms or points of departure on the curve.

Analysis of the comparative positions of the various points in the graph, especially of their deviations from the synthetotypical condition, should be undertaken by taking that condition as the origin of the coordinates. If the points on the curve represent comparably primitive types, while those equally distant from the curve represent the same degree of deviation, then it seems natural to use the curve itself, the canonical line, as a new abscissal axis. Then for values of the ordinate oriented significantly with respect to this new abscissa we must select the line that is perpendicular to that abscissa (the canonical line) on a logarithmic graph.

By means of these two coordinates we can undertake an analysis of the deviations of the various forms in the course of their history. We shall call the longitudinal direction (in the direction of the calculated line) *extension* and the deviation from it (away from that line) *dispersion.* Not having a satisfactory evolutionary unit or quantum for measurement of rates of transition from one form to another, we shall use an arbitrary graphic unit

that permits division of the field into small curvilinear quadrates which outline the particular complexes studied within the whole constellation of values. The use of such an artifice permits us to evaluate the comparative extensions and dispersions of the various forms involved.

Even such a superficial examination reveals the progressive way in which the carnivores have broadened their ecological scope in the course of time. Special study of extensions and dispersions permits recognition of the detailed course of such ecological conquests and establishes the fact that maximal expansion occurred in the Pontian-Pliocene, a time surely coinciding with the climax of the mammals. (See fig. 9.) Tables 3 and 4 give the extreme values for extension and dispersion and illustrate the course of the range of variation of those characteristics. Similarly tables 5 and 6 show how the distribution of the forms in question occurred in the course of time and in the two directions: extension and dispersion.

All this leads us to the conclusion that the phenomenon of diversification in the fissipeds, from a comparatively homogeneous original stock, took place in a progressive way by a harmonious advance along

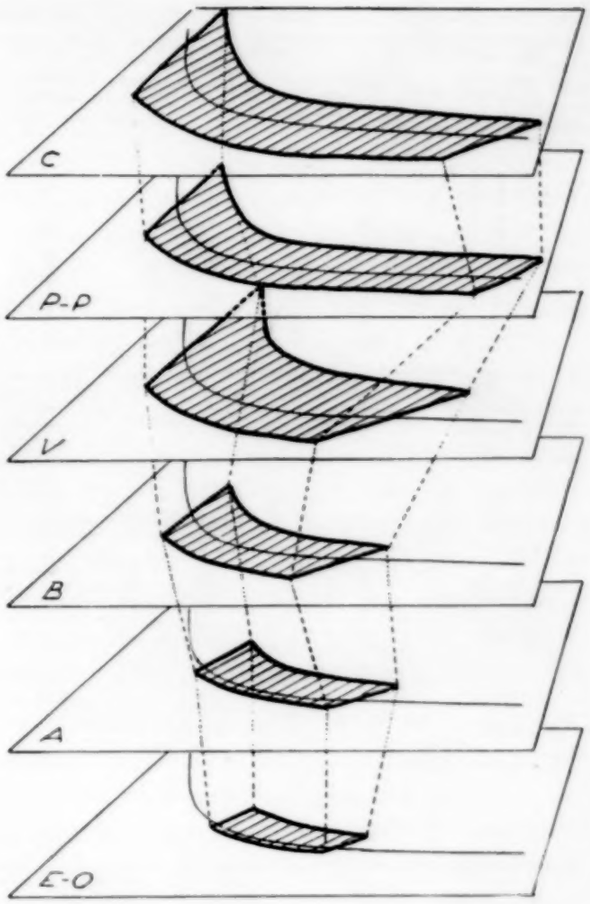


FIG. 9. Changes through time of the graphic area (graph as in figs. 7–8) occupied by fissiped carnivores. E.-O., Eocene-early Oligocene. A., Aquitanian. B., Burdigalian. V., Vindobonian. P.-P., Pontian-Pliocene. C., Pleistocene-Recent.

TABLE 3. *Extension*

| | Eocene-Oligocene | Aquitanian | Burdigalian | Vindobonian | Pontian-Pliocene | Pleistocene-Recent |
|---|---|---|---|---|---|---|
| Observed limits | +4.30 to −2.60 | +4.90 to −4.00 | +5.80 to −5.40 | +7.50 to −8.00 | +12.50 to − 8.00 | +12.80 to − 9.00 |
| Direction | +1.70 | +0.90 | +0.40 | +0.50 | + 4.50 | + 3.80 |
| Range | 6.90 | 8.90 | 11.20 | 15.50 | 20.50 | 21.80 |
| Increment | 0 | +2 | +2.30 | +4.50 | + 5 | + 1.30 |
| Cumulative increment | 0 | 2 | 4.30 | 8.60 | 13.60 | 14.90 |

TABLE 4. *Dispersion*

| | Eocene-Oligocene | Aquitanian | Burdigalian | Vindobonian | Pontian-Pliocene | Pleistocene-Recent |
|---|---|---|---|---|---|---|
| Observed limits | +1.70 to −1.30 | +3.00 to −0.80 | +2.80 to −2.50 | +1.90 to −2.50 | +2.50 to −2.00 | +2.20 to −2.20 |
| Direction | +0.40 | +2.20 | +0.30 | −0.60 | +0.50 | 0 |
| Range | 3.00 | 3.80 | 5.30 | 4.40 | 4.50 | 4.40 |
| Increment | 0 | +0.80 | +1.50 | −0.90 | +0.10 | −0.10 |
| Cumulative increment | 0 | 0.80 | 2.30 | 1.40 | 1.50 | 1.40 |

TABLE 5. *Distribution in extension through time*

| | Eocene-Oligocene | Aquitanian | Burdigalian | Vindobonian | Pontian-Pliocene | Pleistocene-Recent | Totals |
|---|---|---|---|---|---|---|---|
| Zones+ | | | | | | | |
| 13 | 0 | 0 | 0 | 0 | 1 | 2 | 3 |
| 11–12 | 0 | 0 | 0 | 0 | 3 | 4 | 7 |
| 9–10 | 0 | 0 | 0 | 0 | 3 | 10 | 13 |
| 7–8 | 0 | 0 | 0 | 1 | 0 | 5 | 6 |
| 5–6 | 1 | 1 | 1 | 0 | 2 | 0 | 5 |
| 3–4 | 2 | 2 | 1 | 2 | 3 | 4 | 14 |
| 1–2 | 10 | 3 | 4 | 4 | 1 | 13 | 35 |
| Totals | 13 | 6 | 6 | 7 | 13 | 38 | 83 |
| % above | 4.8 | 31.6 | 31.6 | 21.2 | 40.6 | 52.1 | |
| Zones− | | | | | | | |
| 1–2 | 5 | 9 | 3 | 4 | 5 | 16 | 42 |
| 3–4 | 1 | 4 | 8 | 13 | 4 | 4 | 34 |
| 5–6 | 0 | 0 | 2 | 8 | 7 | 3 | 20 |
| 7–8 | 0 | 0 | 0 | 1 | 3 | 9 | 13 |
| 9 | 0 | 0 | 0 | 0 | 0 | 3 | 3 |
| Totals | 6 | 13 | 13 | 26 | 19 | 35 | 112 |
| % below | 31.6 | 68.4 | 68.4 | 78.8 | 59.4 | 47.9 | |

TABLE 6. *Distribution in dispersion through time*

| | Eocene-Oligocene | Aquitanian | Burdigalian | Vindobonian | Pontian-Pliocene | Pleistocene-Recent | Totals |
|---|---|---|---|---|---|---|---|
| Zones+ | | | | | | | |
| 3 | 0 | 2 | 1 | 1 | 2 | 4 | 10 |
| 2 | 1 | 2 | 1 | 6 | 6 | 12 | 28 |
| 1 | 14 | 9 | 4 | 10 | 5 | 20 | 62 |
| Totals | 15 | 13 | 6 | 17 | 13 | 36 | 100 |
| % above | 78.9 | 68.4 | 31.6 | 51.5 | 40.7 | 49.3 | |
| Zones− | | | | | | | |
| 1 | 3 | 6 | 9 | 12 | 7 | 24 | 61 |
| 2 | 1 | 0 | 3 | 3 | 11 | 11 | 29 |
| 3 | 0 | 0 | 1 | 1 | 1 | 2 | 5 |
| Totals | 4 | 6 | 13 | 16 | 19 | 37 | 95 |
| % below | 21.1 | 31.6 | 68.4 | 48.5 | 59.3 | 50.7 | |

both branches in such a way that the presence of an isolated form in an extreme position in the direction of extension may be balanced by the existence of a group of forms with relatively slight extension and placed on the opposite branch.

It is possible to find a relationship between the evolutionary paths followed by the two processes of divergence. The geometric mean, a measure of divergence, gives us a clear idea of the total phenomenon through time: a progressive and constant increase in ecological scope. (See table 7 and fig. 10.) The fact of the spread of new forms into hitherto unoccupied niches has a very impressive reflection in the tables and the graph. If, for example, we compare the densities in

outer parts of the band with those along the calculated curve of the norm, we note systematic increase in the measurement involved (an index of diversification). The significance of this lies in the increasing importance of specialized types relative to that of the canonical forms near the calculated curve. Tables 8 and 9 reveal such changes.

The number of canonical forms (those along theoretical curve) is only 26. The number with positive dispersion (above the curve) is 88, and that with negative dispersion (below the curve) is 81. The approximate equality of these figures shows that even for centrifugal spread there is a clearcut symmetry of distribution. On the other hand, it is evident that the greater number of the forms involved are in the immediate neighborhood of the new coordinates if not quite on the calculated curve itself. The first row of quadrants on each side of the curve includes as many as 135 forms, all together more than two-thirds of the total.

Those facts demonstrate the reality of the symmetrical arrangement around the values considered primitive. It has already been noted that the means for the value of $\alpha$ in various faunal associations, carried out separately by collecting sites, tend toward the value 45°. For $\beta$ we have only had the value for one association, the mean of which also is approximately 22.5°. This fact clearly suggests some degree of numerical control of the specialized variants by the evolutionary tendency indicated among the primitive forms, which seems perhaps to argue for the idea of orthogenesis.

TABLE 7. *Total divergence in terms of extension and dispersion*

| | Eocene-Oligocene | Aquitanian | Burdigalian | Vindobonian | Pontian-Pliocene | Pleistocene-Recent |
|---|---|---|---|---|---|---|
| Range of dispersion ($A_D$) | 3.0 | 3.8 | 5.3 | 4.4 | 4.5 | 4.4 |
| Range of extension ($A_E$) | 6.9 | 8.9 | 11.2 | 15.5 | 20.5 | 21.8 |
| Index of divergence ($\sqrt{A_D \quad A_E}$) | 4.5 | 5.8 | 7.7 | 8.2 | 9.5 | 9.8 |
| Increment | 0 | +1.3 | +1.9 | +0.5 | +1.3 | +0.3 |
| Cumulative increment | 0 | 1.3 | 3.2 | 3.7 | 5.0 | 5.3 |

TABLE 8. *Diversification in terms of extension*

| | Eocene-Oligocene | Aquitanian | Burdigalian | Vindobonian | Pontian-Pliocene | Pleistocene-Recent | Totals |
|---|---|---|---|---|---|---|---|
| Zones outside ± 4 (A) | 1 | 1 | 3 | 10 | 19 | 36 | 70 |
| Zones within ± 4 (B) | 18 | 18 | 16 | 23 | 13 | 37 | 125 |
| Index of diversification (A/B) | 0.05 | 0.05 | 0.18 | 0.43 | 1.46 | 0.98 | 0.56 |

TABLE 9. *Diversification in terms of dispersion*

| | Eocene-Oligocene | Aquitanian | Burdigalian | Vindobonian | Pontian-Pliocene | Pleistocene-Recent | Totals |
|---|---|---|---|---|---|---|---|
| Zones outside ± 1 (A) | 2 | 4 | 6 | 11 | 20 | 29 | 72 |
| Zones within ± 1 (B) | 17 | 15 | 13 | 22 | 12 | 44 | 123 |
| Index of diversification (A/B) | 0.12 | 0.26 | 0.46 | 0.50 | 1.66 | 0.65 | 0.38 |

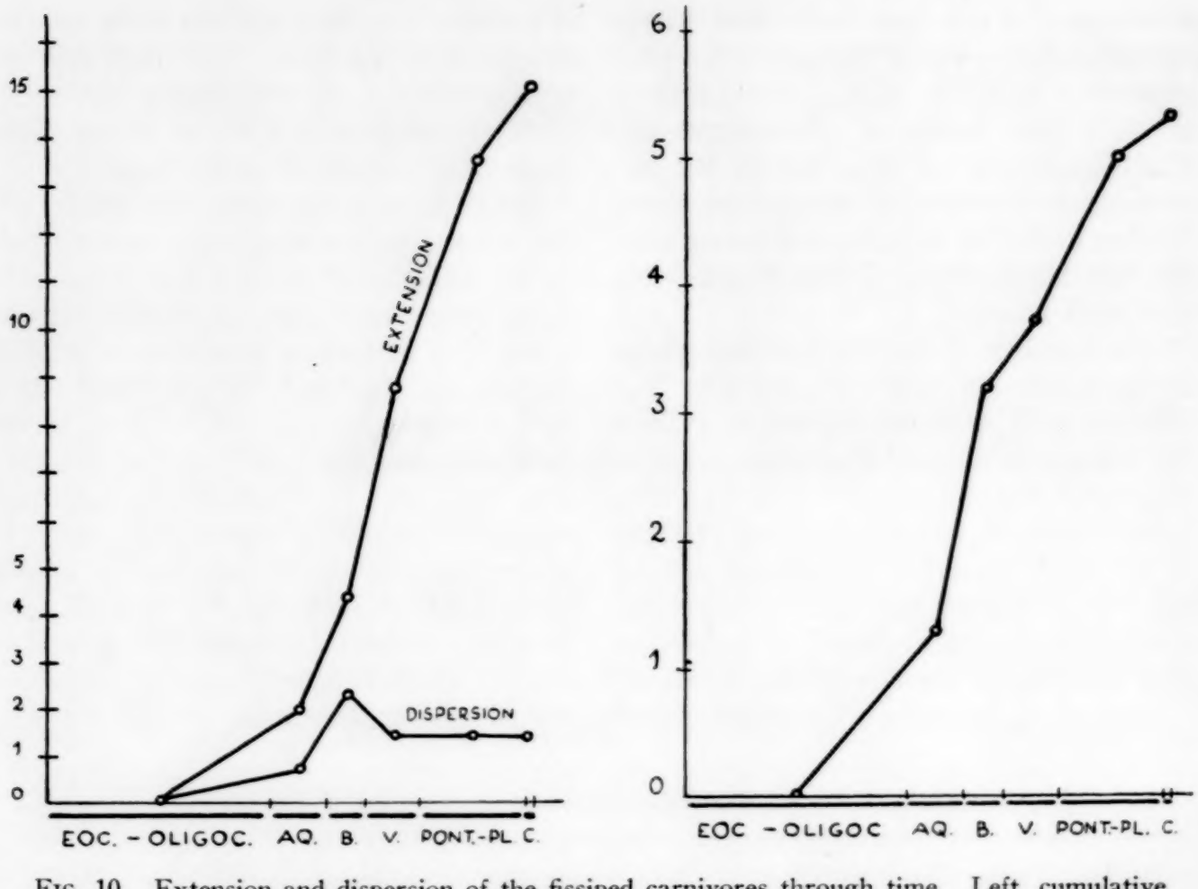


FIG. 10. Extension and dispersion of the fissiped carnivores through time. Left, cumulative increments (see tables 3 and 4). Right, index of divergence (see table 7). Eoc.-Oligoc., Eocene-early Oligocene. Aq., Aquitanian. B., Burdigalian. V., Vindobonian. Pont.-Pl., Pontian-Pliocene. C., Pleistocene-Recent.

## POSITIONS OF THE FAMILIES

From the study of the graph can be deduced with considerable accuracy the whole history of the fissiped carnivores and the process of their diversification into families, genera, and species, departing from the basal types near the primitive values. Unless there is something misleading in the regularity of the graphic distribution of the points, it is understandable that it will be practicable to deduce the phylogeny of each particular group of carnivores. That is, indeed, the case and therefore the study of the graph must make possible comparatively easy interpretation of the various phyletic sequences. The biological process of evolutionary radiation of the families in the course of time is effectively represented in the graph by a centrifugal tendency of the corresponding evolutionary lines.

In some instances the graph cannot distinguish and delimit neighboring biological series due to the phenomenon of convergence, difficult to analyze numerically. Nevertheless the graph does succeed in giving us an excellent over-all view of fissiped history, in many instances in agreement with the history reconstructed by previous authors and that agreement, after all, is a clear proof of the validity of the proposed schema.

In the following we shall undertake examination of the graph with respect to each family and shall compare it with current concepts.

*The Polymorphic Basal Group.* There is general agreement on placing *Cynodictis* and neighboring Eocene and Oligocene genera at the base of the fissiped carnivores. From this group, surely homogeneous and very plastic genetically, the fundamental types of the various families

radiate, particularly the canids and viverrids as the stages nearest to the basal structure.

The graph shows the reality of this grouping. The forms that Teilhard called cynodictoids, cynodontoids, and stenoplesictoids and that Boule grouped together in the family Cynodictidae appear, indeed, on the graph surrounded by the areas of the canids and viverrids.

The situation of the various genera is completely regular. This is a group of carnivores with slight divergence from the norm. The different values of extension of the various forms already indicates the earliest functional specialization in the directions of types anticipatory of the appearance of the whole complex of families that are to become secondary centers of later specialization.

Some authors give the whole group the taxonomic rank of a family. In accord with Simpson and some other authors, we find it convenient to divide the group in accordance with the essential lines of divergence that appear from the beginning.

The group comprising *Cynodictis, Cynodon, Pachycynodon, Cephalogale,* and other genera, situated in the canid area and with pre-canid characters, is included in the Canidae and is made a distinct subfamily.

Some of the forms that make up the cynodontoid and stenoplesictoid groups of Teilhard should be referred to the Mustelidae, a family in which the fundamental types retain essential traces of those forms. Some stenoplesictoids point toward the viverrid line and therefore should be placed in that family, while others adumbrate the felids and therefore are incorporated in the Felidae by us.

*Canidae.* The area of the canids occupies a rather central position, which was to be expected from the primitiveness of the group. The graphic constellation is scattered over the four quadrants, although with decided concentration in the second and fourth quadrants as defined by normal Cartesian coordinates with origin at the synthetotype (fig. 8). The canonical index[4] (30.9%) confirms the stated primitiveness. The extreme values of $\alpha$ and $\beta$ define an equidimensional area in which the index b/a[5] is 98.8. The dispersion lies between + 2.7 and − 2.4 and the extension between + 1.2 and − 3.9, both measured in the arbitrary units previously mentioned. Its primitiveness gives this family a certain homogeneity, which is nevertheless compatible with moderate specialization of the various forms.

The graph shows various centers of concentration which correspond in a general way with the taxonomic situation. (See fig. 11). Aside from the subfamily Cynodictinae, right on the canonical line, the group that still retains structural primitiveness with comparative faithfulness is that of the Caninae. This is a bradytelic group that retains fully mesocarnivorous characters. Simpson goes so far as to consider its present members as virtually late Eocene fissipeds, and on that basis includes the forms of the basal complex in the Caninae.

We include in the Caninae some genera (*Cuon, Temnocyon,* etc.) that Matthew and Simpson place with *Simocyon,* a canonical form with hypocarnivore tendencies which, according to Simpson, constitutes a separate subfamily.

The subfamilies Amphicyoninae and Hemicyoninae (= Amphicyondontinae) have a markedly hypocarnivorous tendency on account of which some authors (e.g., Pilgrim) have considered them related to the ursids. The values of the two angular measurements nevertheless are such as to separate them from that family. The two subfamilies, which we may call paraursoid, are clearly distinguished by

[4] The canonical index is defined as the ratio (in percent) between the number of forms that are on the canonical line, or practically so, and the total number of forms in the pertinent family or subfamily.

[5] This index measures the relative values of dispersion and extension. It is defined as 100b/a, in which b is the absolute amplitude of dispersion (measured in the arbitrary units here used) and a is the absolute amplitude of extension.

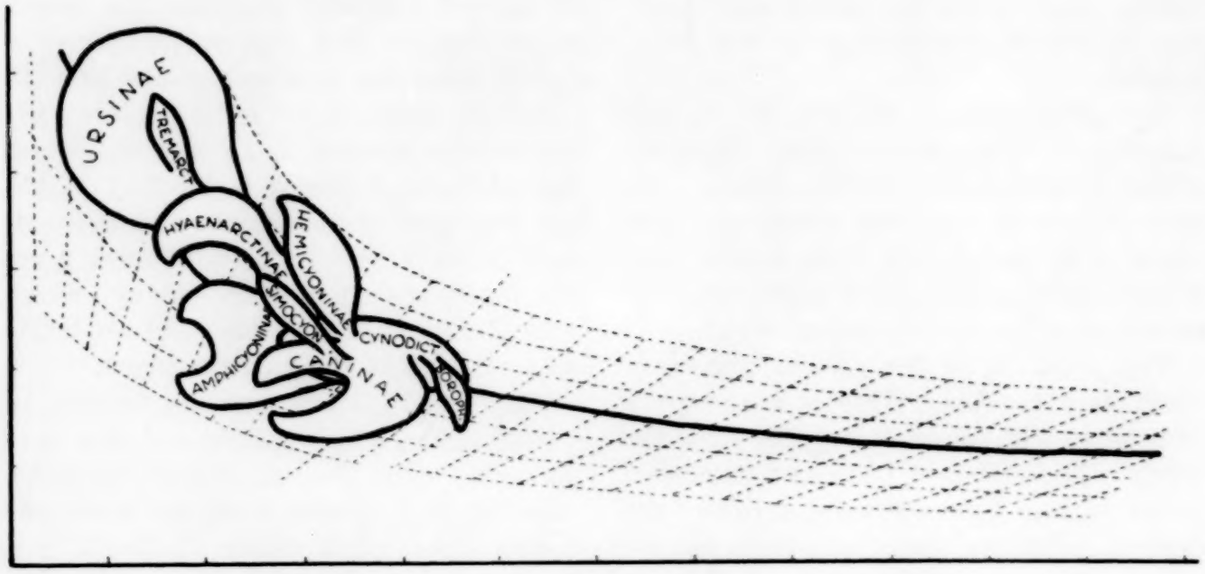


FIG. 11. Phylogenetic distribution of the Canidae and Ursidae on the graph (as in fig. 8).

their positions on the graph. The Hemicyoninae have positive dispersion, like *Cephalogale* with which they seem to intergrade, and the Amphicyoninae have negative dispersion.

The subfamily Borophaginae, with convergence toward the hyaenids, logically occupies a well defined position on the aeluroid branch of the curve.

*Ursidae.* The ursids appear late in the evolutionary history of the carnivores and their relationship with the canids is evident. Morphologically and physiologically their characters are stressed in the hypocarnivorous direction. The ursids occupy the extreme places on the arctoid branch of the curve (fig. 11).

The index b/a = 76.1 shows that the area of the ursids is almost equidimensional. All their forms are on the arctoid branch and almost all in the second quadrant. The extension lies between − 3.3 and − 8.2 and the dispersion between + 2.6 and − 1.2. Only the genus *Ursus* shows a tendency toward negative displacement. The canonical index of 7.7% is low.

In the graph distinctly separate groups are not evident. The positive dispersion within the group seems to indicate relationship or convergence with the Hemicyoninae, a fact already recognized by previous authors.

We observe in the graph two rather salient lines: that of *Ursavus-Ursus* and that of *Hyaenarctos-Indarctos.* We have not been able to deduce from simple examination of the graph whether the two branches represent as many subfamilies, but there is indeed a certain separation between them. Similarly *Tremarctos* seems to represent an isolated group between the two branches.

*Procyonidae.* Hypocarnivorous like the ursids, the procyonids apparently were earlier in becoming distinct from the primitive carnivorous stock. It is the general opinion that they arose from the basal canid zone. Their omnivorous specialization, along with other morphological details, suggests the ursids and justifies the appellation of subursids by which they are also known.

We are not in a position to examine the position of this family critically for lack of data. However, the few goniometric data that we do have confirm current ideas as to the nature of the group. Some characteristically conservative genera, such as *Bassaricyon,* are indeed near *Cynodictis.* On the other hand *Procyon* and *Phlaocyon,* at the extreme of omni-

vorous specialization, are near the arctoid pole of the graph.

The distribution of points on the graph will perhaps make it possible, with more data than now available, to carry out a critical enquiry into the possible polyphyletic nature of the group.

*Mustelidae.* The mustelids are the most polymorphic fissiped family. This heterogeneity is shown in a diversity of specializations so great that the convenience of splitting the group into several wholly distinct families should perhaps be considered. There is much convergence in its forms and its taxonomic study is consequently rather difficult.

The area occupied is large longitudinally, with the index $b/a = 58.7$. The great majority of forms is within the second quadrant, although they are appreciably present in the other quadrants. As a consequence, in spite of the markedly arctoid character of the family, it is possible to note the presence of a mesocarnivorous section occupied by primitive forms. The extension of the whole area is between $+3.2$ and $-8.9$, the dispersion between $+4.6$ and $-2.5$. The canonical index is 34.4%. That of the Mustelinae and Plesictinae together is as high as 48.5%.

The graphic grouping of the Mustelidae reflects the presence of centers of differing specialization (fig. 12). It is evident that there is a conservative nucleus with the Plesictinae and Mustelinae and another specialized in the arctoid direction in which some forms have positive dispersion (Lutrinae) and others negative (Melinae, etc.).

Much as in the case of the canids, we have separated the primitive and canonical forms as the subfamily Plesictinae, removing them from the Mustelinae of Pilgrim and of Simpson. Some authors (e.g. Schlosser) have united these types with the primitive viverrids in a subfamily Stenoplesictinae.

The Mustelinae are directly derived from the preceding. Their relationship with the Plesictinae is analogous to that between the Cynodictinae and the Caninae. Without losing their distinguishing stamp of comparative primitiveness, the Mustelinae seem to have started in a small scale along the lines of divergent specialization of the family as a whole.

The Mellivorinae, whose position between the Mustelinae and the specialized group of the Melinae-Lutrinae is well known, reflect that biological fact on the graph.

The two latter subfamilies seem to be sharply distinctive. The Melinae have negative dispersion while the Lutrinae have positive dispersion, with some in-

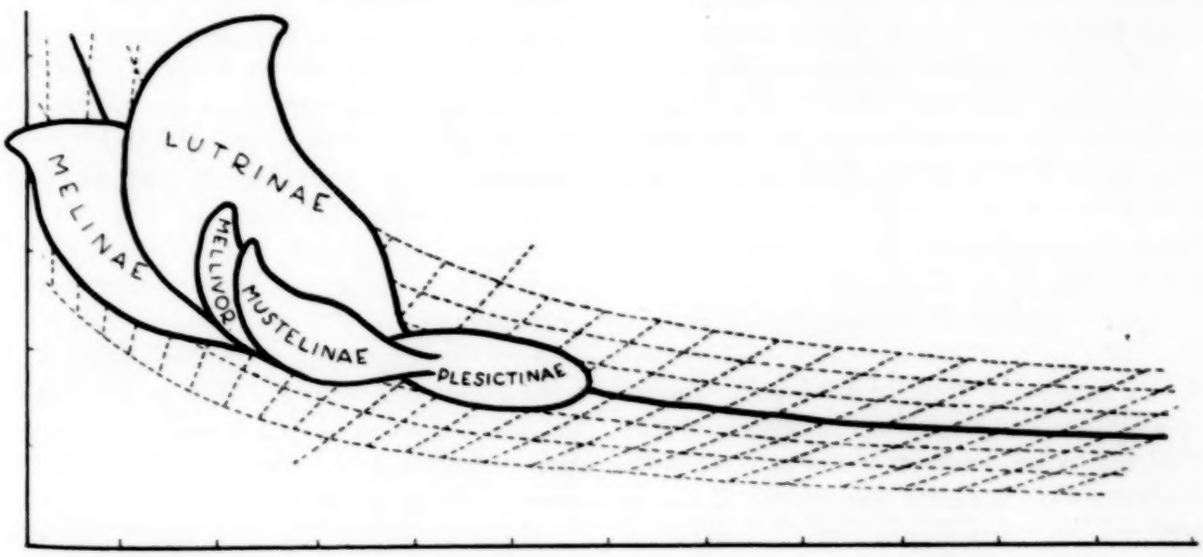


FIG. 12. Phylogenetic distribution of the Mustelidae on the graph (as in fig. 8).

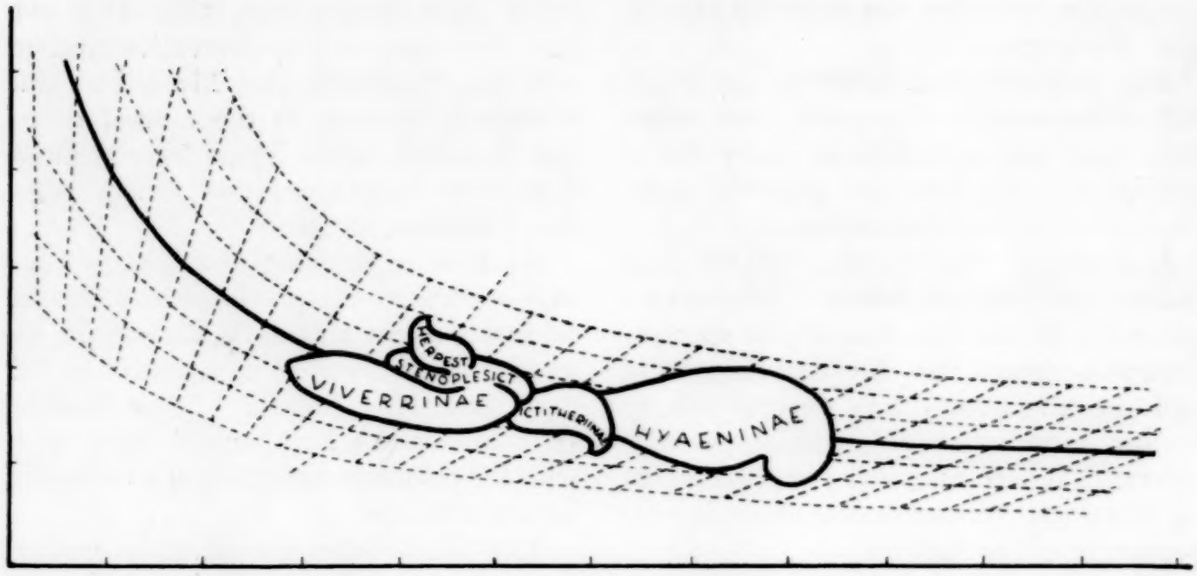


FIG. 13. Phylogenetic distribution of the Viverridae and Hyaenidae on the graph (as in fig. 8).

tergrading. The former have, furthermore, the lowest values of extension of all the carnivores. (The angle $\alpha$ of *Meles* is only 4°.)

There remains the group of the Mephitinae, closely related to the Melinae and therefore expectably situated alongside the latter subfamily.

*Viverridae.* Like the canids, the viverrids represent the most primitive types of fissipeds. Just as the canids constitute the point of departure for the diversification of the arctoid branch, the viverridae play an analogous role for the aeluroid branch. This is a family with primitive characters but with a slight tendency toward hypercarnivorous displacement.

This primitiveness and the homogeneity of the group give it a rather reduced area on the graph, the smallest of the complex. The index b/a is 62.5. Extension is between the limits + 2.2 and − 1.7 and dispersion between + 1.5 and − 1.0, which reveals a slight predominance of positive trends. The canonical index is 46.2%.

We assign the rank of subfamily (Stenoplesictinae) to the group including viverroid forms of Teilhard's stenoplesictoids. Its members lie along the canonical curve and are in some degree more hypercarnivorous than the rest of the family.

The Herpestinae represent primitive types of the group, still retaining ancestral characters. Their role in the family is much like that played by the Caninae and Mustelinae in their respective families.

The central group of the family, the Viverrinae, are split around two centers. On the hypocarnivorous side is situated the *Viverra* group and on the opposite side the *Genetta* group, with related genera among which are those transitional to the hyaenids (Fig. 13).

*Hyaenidae.* Like the ursids, the hyaenids appear late in the evolutionary history of the carnivores as a whole. The group overlaps the viverrid branch and surrounds its aeluroid pole. Zittel considered the hyaenids as mere differentiated viverrids, connected to the viverrids, proper, by well defined transitional forms. Simpson drew attention to the analogy between Canidae-Ursidae and Viverridae-Hyaenidae and to the roles played by the transitional genera *Agriotherium* and *Ictitherium.*

This family occupies an elongated area with index b/a = 45.8. The extension is between + 1.0 and + 7.2 and the dispersion between + 1.7 and − 1.2. The canonical index is 26.7%.

The two branches that make up the family, Ictitheriinae and Hyaeninae, are

seen to be well separated on the graph. The former is so placed as to form the connection with the Viverrinae, while the latter has a high degree of positive extension which causes it to come in contact with the Felidae (Fig. 13).

*Felidae.* The felids represent the highest degree of carnivorous specialization in that they, all alone, occupy the aeluroid extreme of the graph. The characteristic peculiarities of the family and its relationships with its allies are fully reflected in the distribution of points on the graph.

The felids occupy an elongated area with index b/a = 40.6. The extension is between + 2.3 and + 12.9 and the dispersion between + 2.8 and − 1.5, which shows that the whole is distributed in the first and fourth quadrants. The canonical index is rather low: 17.6%.

On the graph two zones stand out clearly: one representing the primitive nucleus still united to the basal group and overlapping the region of the hyaenids; the other beginning with the primitive Nimravinae and ending in the true cats. Between the two groups there is a small empty space which prevents observation of the phylogenetic relationships between them.

The primitive nucleus is represented by the Proailurinae, morphologically continuous with the Stenoplesictinae and Plesictinae. Some authors have united them with the mustelids (Schlosser) or with the viverrids (Mivart), while nevertheless accepting the felid direction of their evolutionary trend. In general, however, they have been placed at the base of the felids (Flower, Pilgrim, Simpson), their viverroid characters being considered as indications of the primitiveness of the group.

The Nimravinae are situated completely within the felid area, representing a chronological anticipation of the true cats. The Felinae occupy the extreme end of the graph, which is partly shared with the Nimravinae and the Machairodontinae. Whether or not they are derived from the Nimarvinae, the Felinae are in contact with the latter on the graph and have similar values of $\beta$.

The Machairodontinae form a rather compact block within the area occupied by the Felinae and have, curiously enough, a canonical index (40%) considerably higher than that of the Felinae (5%). If the Machairodontinae are derived from the Nimravinae, as some have thought, that would find quite acceptable possible confirmation in the graph. (Fig. 14.)

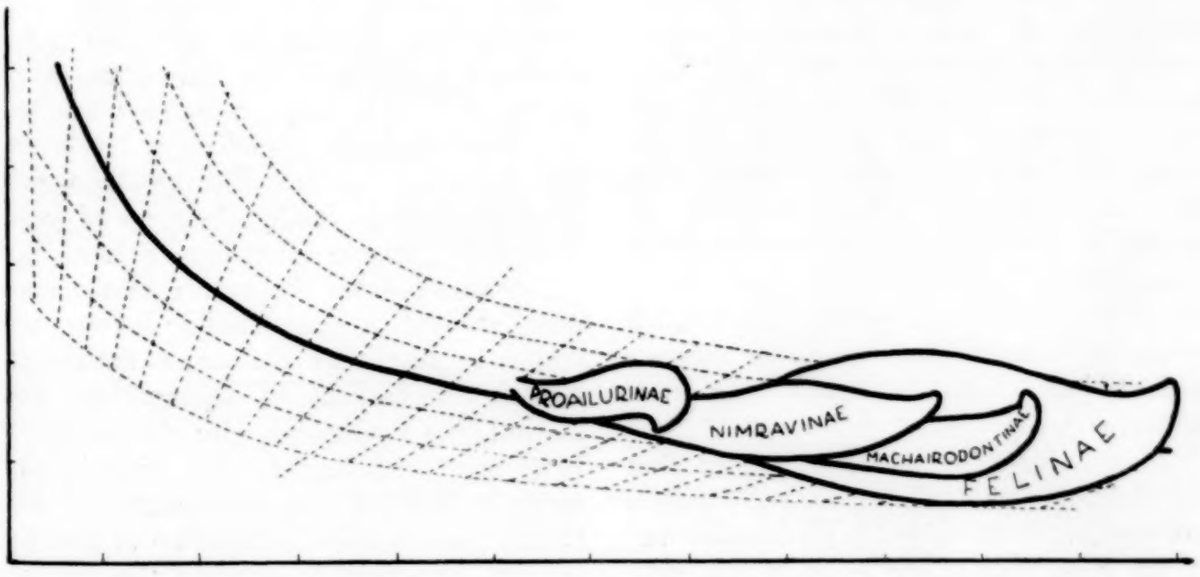


FIG. 14. Phylogenetic distribution of the Felidae on the graph (as in fig. 8).

## Conclusions

Observation of the history of the carnivores through the present study seems to throw new light on the mechanism of the phenomenon of expansion in that group. The expansion has occurred from a basal complex in the Eocene, where the complex has a certain effective homogeneity along with an evident initial polymorphism. This polymorphism affects not only the individuals but also the species, in such a way that there are gradual, imperceptible transitions between some species and others, making difficult the establishment of the usual systematic limits between them. Study of the Eocene forms gives the impression that there exists almost complete morphological continuity within the fissiped carnivore complex, suggesting that there was a small group with a variability so enormous that it embraced prearctoid as well as preaeluroid types. This continuity has already been stressed previously (Teilhard), but our observations, based on measurements of the angles $\alpha$ and $\beta$, demonstrate it in a quantitative way.

Study of the graph seems to show clearly that in the first phase there appears a great richness of types which presage the extensive subsequent diversification. This is surely a phase of mutations adequate to give rise by discontinuous steps to the various basic types, representing what has been called the "basic radiation" of the main branches. These types recombine and determine trends along the indicated paths, whether with the intervention of natural selection or thanks to the action of the environment. Subsequently new mutations give rise to the various subgroups within each branch originally created and mould the characteristics of those branches into new patterns.

This conception seems to imply that the definitive traits of the various families are essentially contained in a potential way in the genotypes of the initial forms, submitted to continuous modifications by chromosome mutation. According to this view, the evolution of the group in its essential outlines must already have been defined at its beginning through a great richness of pre-specialized types. A later mutational phase determined the precise outlines of the structures created. This way of looking at things somewhat depreciates the "creative" role of the secondary mutations in favor of the primary mutations, endowed with considerable innovational potency which determined the course of subsequent evolution.

This schema hints at the existence of a mechanism of typological diversification basic to a process of segregation of characters in a group of great initial polymorphism. This process has been called "lysis" by Blanc and is exactly the picture of the evolutionary process that he puts forward, which also seems suitable in our case and in accordance with the observations made by us.

The initial polymorphism of Blanc undoubtedly exists in our basal group of Paleogene carnivores. This polymorphism is susceptible to simplification and to resolution into single lineages and sequences progressively more homogeneous and more clearly defined. Our example presents an instance comparable with those of evolution by *cosmolysis*. The preapogean and apogean phases of Blanc appear, however, as if superimposed and run together, bearing in mind the considerable duration of the Paleogene, here represented by a single complex made up by forms evidently at different levels on the temporal scale. The postapogean phase represents, finally, the stage of fixation of the branches that have arisen.

Obviously, from the nature of the material studied, it is impossible in our example to recognize the exact details of Blanc's mechanism of segregation, but the existing agreement with that author's ideas must be accepted. He, himself, has recently pointed out agreement of his theory with Vavilov's doctrine of genetic centers, proposed to explain the mechanisms of expansion and differentiation of

plant species starting from comparatively restricted geographic areas. Vavilov's idea is based on phenomena comparable to those of segregation of characters and to the principle of original mixture of differential characters, and it represents in space what we have followed through time in the Order Carnivora.

The ideas of Blanc and Vavilov, then, suggest to us the interpretation adopted for the biological evolution of the group studied. The scanty signposts available in paleontology as guides for deduction seem, even in our example, sufficiently clear to inform us of the probable reality of the road followed.

Our study shows, furthermore, that the progress of the evolutionary phenomenon occurs in company with a marked tendency for ecological expansion of the group in question. Diversification occurs in the form of a fan, a form exemplified in our instance by a graphic pattern which suggests, indeed, the ribs of a fan. Such a process produces a kind of lysis or pulverization of functions and structures formerly connected, which occurs around the directive axis approximately defined by the median value, as if there were an attempt to retain the point of departure of the complex.

This progressive diversification constrained by a median value that corresponds approximately with the original type is a fact already known in recent populations thanks to the Mendelian principles. Moreover, the idea of expansion through time of evolutionary lineages symmetrically on each side of an axis has already been suggested in theoretical or merely qualitative studies, such as are most of those in the field of broad evolutionary processes. Nevertheless our observations based on practicable angular measurements permit us to affirm the reality of this principle and to support it for the first time on a quantitative basis.

It is quite possible that such a mode of evolution of certain groups, departing from basic complexes undergoing energetic mutagenic influences, which give rise in them to a broad polymorphism without destroying the homogeneity of the complex, may be a fact common to the majority of mammalian orders. This may possibly be one of the usual roads, one of the most common norms, of organic evolution. In the meantime, the concepts of Blanc and of Vavilov seem to have clear application to such instances. The segregation of characters in such groups is a real fact which subsequent studies must trace with greater clarity in order to establish its true degree of generality. Nevertheless we believe that we have obtained, even if for a single and particular group (but a typical one), a first numerical illustration of these ideas. We offer it as a contribution to knowledge of the mechanism of evolution as it occurs in the basal stocks of a group both homeogeneous and polymorphic at the same time, at the critical moment of the opening of divergent pathways which are eventually to give it its ecological scope and the mastery of its greatest possibilities of expansion.

## Summary

Within the field of a special branch of biometry, which the authors call masterometry, two angular dimensions are established, $\alpha$ and $\beta$, measured, respectively, on the lower and upper carnassial teeth of fissiped carnivores. The angle $\alpha$ is measured on a projection of the labial side of the tooth between a straight tangent to the base of the enamel of the crown and another line tangential to the tip of the main cusp and that of the talonid. The angle $\beta$ is measured on an occlusal projection between a straight line passing through the metacone and the most anterior point of the tooth and another through the metacone and the protocone.

The systematic evaluation of these measurements uses as a point of departure the values for a basic Eocene form, *Cynodictis,* which the authors designate a *synthetotype*. The values of $\alpha$ and $\beta$ of the synthetotype are, respectively, 45° and

22.5°. The various forms of all the families of fissipeds are distributed around these values in a perfectly regular way.

In the constellation of fossil and recent forms here studied, the relationship between $\alpha$ and $\beta$ is a negative correlation expressable by a regression line the equation of which represents a polytropic curve. Around this curve there is constructed a system of coordinates with the origin at the synthetotypical values, the biological significance of which is apparent. Distribution of other values around that origin is in a pattern that is regular both from a phylogenetic and from a systematic point of view. Furthermore, in the evolutionary history of the group there is visible a progressive widening of the area occupied on the graph, which is equal to a progressive ecological conquest by the group as a whole and by means of appropriate specializations.

The forms of any one biocenosis are distributed around a mean equal to the synthetotypical value; the dispersion of other values is harmonious and is systematically distributed along the graph; and there is a progressive widening of the ecological scope of the group. These facts suggest to the authors that the fissiped carnivores have undergone an evolutionary radiation by *lysis*, similar to that involved in the theories of Vavilov, as regards space, and of Blanc, as regards both space and time.

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# NOTES AND COMMENTS

## SYMPOSIUM ON EVOLUTION HELD IN SPAIN

G. G. Simpson

*The American Museum of Natural History, New York*

With few exceptions, American students of evolution are remarkably unanimous in their basic philosophical and theoretical positions. In their non-scientific life they may subscribe to a supplementary (or even to a contradictory) philosophy, but their philosophical approach to actual problems of evolution is almost invariably naturalistic. They may disagree vehemently as to details, but there are few who do not adopt the synthetic theory of evolution as their general base. The relationship between evolution and theology is still discussed outside the strictly scientific sphere, but few of the serious evolutionists in this country consider it a legitimate technical problem. The most common attitude toward vitalism and finalism is that those schools are now so old hat as to merit no serious consideration. The problem of continuity *versus* saltation in evolution is not wholly forgotten, thanks almost entirely to Goldschmidt and a few of his students, but the majority of American evolutionists now approach it with a *parti pris*, if at all. Such wide agreement has its useful, desirable aspects. It can, however, generate a provincial complacency.

The fact is that many European evolutionists just as accomplished as any in America do not consider those questions closed and give quite different answers from those of the American majority. It behooves us to recognize that fact. In this connection a summary of a symposium on evolution[1] recently held in Spain may be of interest. The chair was occupied by Professor Jean Piveteau, who also spoke at length. Other principal speakers were Father F. M. Bergounioux, Dr. Bermudo Meléndez, and Dr. M. Crusafont Pairó. Drs. Jean Viret and Piero Leonardi made brief remarks. It need hardly be said that all of these gentlemen are distinguished scientists and that each has a very substantial body of published work in the field of evolution, both descriptive and theoretical.

Three of the four main speakers (Piveteau was the exception) made a strong point of the compatibility of evolution with Roman Catholic theology. The tenor is sufficiently shown by a translation of remarks by Meléndez:

"It is possible to be an evolutionist and a very good Catholic, without one of these having anything whatever to do with the other. Indeed Father Bergounioux made a statement that coincides precisely with my way of thinking: 'Who doubts that God can work miracles and does work them? But He does not work them capriciously, He does not amuse himself in this way, aside from the need for accepting a miracle because there is a reason for it.' It seems to me, then, wholly childish, as Father Bergounioux said, to suppose that in situations where a miracle is not needed the Divine Providence is going to amuse Itself simply for the pleasure of making things complicated. . . ."

There was evident agreement that evolution is the mechanism of creation inherent in the one necessary miracle of the First Cause, and that its study is an investigation of secondary causes. Crusafont put this neatly: "[The study of evolution] is a matter of demonstrating and establishing the why of the existence of man in this world, into which he has not come just to live and to die but for something higher, because he carries the message that God put into the First Cause in order that later on man should, with his speech, extol this magnificent creation developed by evolution. A creation developed by evolution, thus only one necessary miracle: that of the Creation, the beginning. . . ."

All of the main speakers agreed that evolution is finalistic. Piveteau was the least extreme in this respect: "I believe that, in effect, finalism cannot be considered as the realization of a preconceived end, but that it is to be understood in the light of the analogy with invention. That is to say, the end is not given but is sought." Crusafont presented a more flatly finalistic statement: ". . . Evolution seeks and demands a finality, something to round out its magnificent work. That completion is, of course, man made in the image of God. . . . Evolution has its marvelous end in the recognition of the spiritual world, achieved for the first time by man. . . ."

The speakers agreed, without any dissent, that the major groups, at least, of organisms arose by saltation. Viret's one published re-

[1] Coloquio sobre evolucionismo. Cursillos y Conferencias del Instituto "Lucas Mallada," Fasc. III, pp. 147–169, Madrid, 1956.

The symposium was part of the "II Cursillo Internacional de Paleontología de Sabadell," held at Sabadell, Spain, in July, 1954.

mark was on this subject, with the origin of the Chiroptera as an example: "Most or at least many biologists have presented the appearance of the bats as something that must have been quite gradual. . . . Here is a sort of mental necessity to believe in imperceptibly gradual transformations. Nevertheless nature shows us that this is completely wrong. There is no such thing as a quarter of a bat, or a third of a bat, or a half bat, but all at once there appears a new type apt for flight." Bergounioux, Meléndez, and Piveteau made the same point with different examples.

On the level of microevolution Bergounioux, alone among the speakers, expressed a limited adherence to the synthetic theory and the importance of natural selection. Speaking of mastodonts in what is now Portugal he concluded that competition might have been especially severe there and that, ". . . taking into consideration the synthetic theory of evolution, which we consider less imperfect than the others, the smallest genetic variation might give a mutant individual a certain advantage in perpetuating itself and in adapting itself to the conditions in which it found itself."

These brief, freely translated quotations have not done justice to the full original text. They have perhaps given a hint as to its flavor, and if that flavor seems strange to some readers of this journal, well—that very fact is its great value.

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## THE PALAEOBOTANIST, VOLUME 2, 1953 LUCKNOW

SUZANNE LECLERCQ

*University of Liege, Belgium*

"The Palaeobotanist" is a young review published under the direction of the Birbal Sahni Institute of Palaeobotany at Lucknow. So far, three volumes have been issued, the first of which (1952) was devoted to the memory of the great scientist Birbal Sahni. The second volume is, in fact, the first to show the standing of the review. Its contributors are all Indian and most of them are disciples of Birbal Sahni. In this way and in another manner, the second volume constitutes a new homage to the noble personality of Birbal Sahni and is probably the one he would have liked the best.

The volume consists of 17 contributions. No satisfying summary accounts of their contents can be made as the papers are so various. They go into matters that concern algae, pteridophytes, gymnosperms, angiosperms treating of morphology with suggestions of evolution, theoretical and stratigraphical significance. On the other hand, the contributions deal with geological formations extended from Silurian up to Pleistocene. For that reason a few accounts only can be mentioned in a short report.

The majority of the papers are related with the classical flora of the Rajmahal Series of Bihar. The Rajmahal material contains both impressions and petrified specimens of peculiar interest.

In a clear review of the last twenty years activity, Dr. A. R. Rao [1] shows that new records of plants, in Rajmahals, have established that the flora resembles the Hope-Bay flora rather than that of the Madras Coast as formerly stated. He focuses attention on the fact that the Hope-Bay flora is unique in that it shows some affinities with the Jurassic flora of England on the one side, and with the Indian Jurassic flora on the other. It is therefore of interest to amplify researches along this line as it appears that their results may establish the existence of more closely related links between Indian and Western European flora during Jurrassic time. Among the most interesting data obtained from Rajmahal, the author mentions petrified megastrobilus, coniferous, leafy shoots, small three winged microspores with podocarpeous affinities. These records establish that the Podocarpaceae were much better represented in the Rajmahal flora than stated before. These facts are in conformity with the late Professor Birbal Sahni's suggestion that the Podocarpaceae may be discovered in the Mezozoic rocks of India, and Professor Florin's opinion that *Podocarpus* is definitely a southern genus. The authors test the validity of Florin's conception that from the Permian onwards, the conferous divided into two different groups, one of which had its roots in the northern hemisphere, while the other was markedly southern hemisphere group. This southern group was dominated by the Podocarpaceae.

A study by R. V. Sitholey and M. N. Bose [2]

[1] Rao, A. R., Some Observations on the Rajmahal Flora. Pp. 25–28.

[2] Sitholey, R. V., and M. N. Bose., *Williamsonia santalensis* sp. nov. A male fructification from the Rajmahal Series with remarks on the structure of *Ontheanthus polyandra* Ganju. Pp. 29–39.

focuses attention on peculiar features exhibited by a new species of Williamsonia: W. *Santalensis*. Despite the great resemblance shown with the Williamsonia, the new male fructification differs in possessing fertile linear complex appendages in place of the usual reniform synangia and in having an asymmetric and twisted development of the sterile upper part of the microsporophyll. For the authors these characters are of morphological value and allow the re-interpretation of the structure of the male flower *Ontheanthus polyandra* Ganju, hitherto considered as a unique type differing from the Bennettitales in several important features.

One contribution of M. N. Bose deals with Bennettitales. The paper [3] is a thorough study of 50 specimens of a new species of a stem of Bennettitales *Bucklandia Sahnii* that exhibits peculiar features in its anatomy, mode of branching and position of flowers. The early secondary wood of *B. Sahnii* differs from all the *Bucklandia* of whose anatomy is known in having scalariform tracheids. The branching habit of the new species resembles the mode of branching of *Wielandiella angustifolia* Nathorst in giving off two opposite lateral branches just below the point where flowers were borne. As a consequence of that branching habit, the position of the flower is terminal instead of being lateral. The new species is compared with stem genera belonging to Bennettitales, Cycadeoideas, living Cycads and a specimen formerly described *Homoxylon rajmahalense* which is now considered as a part of the secondary wood of a Bennettitalean stem.

The Pentoxyleae is a new group of Jurassic gymnosperms instituted by Sahni (1948) for isolated stems, leaves and female cones that have been correlated on the indirect but undoubted evidence provided by anatomical structure. As a consequence the group comprises several organ genera: *Pentoxylon, Nipaniophyllum, Carnoconites*. While reconstructing the vegetative parts, Sahni presumed that the flowers of Pentoxyleae were unisexual and borne at the ends of lateral dwarf shoots. The male flower described by Vishnu-Mittre [4] supports this view. *Sahnia nipaniensis* Vishnu-Mittre consists of filiform microsporophylls spirally branched, fused in the basal region to form a disc which surrounds a broad and conical receptacle. The sporangia are unilocular and borne at the ends of short branches of the sporophylls. Pollen grains are monocolpate and boat-shaped. In young flower the microsporophylls are surrounded by a whorl of deciduous bracts. The majority of these characters confirm the Bennettitalean general plan of the male flower. However, unlike the Bennettitales, the microsporophylls remain erect and are fertile to the tip; they are spirally branched and the branches are borne all around the main axis. As in modern Cycads, the sporanges are sac-like and unilocular, and the pollen grains are boat-shaped, with a single furrow. *Sahnia nipaniensis* is believed to belong to the Pentoxyleae on the basis of its apical position on dwarf lateral shoots, the similarity of these with the dwarf shoots of *Pentoxylon Sahnii* and some anatomical characters exactly similar to those of the stems and leaves known to belong to Pentoxyleae. At the same time the investigation of a new collection of *Carnoconites* (female cone) has made it possible to define more accurately the reconstruction of the *C. compactum* made by Birbal Sahni. The contribution of Vishnu-Mittre is of great interest, it adds an important fact to our knowledge of the fascinating Pentoxyleae which defy classification since the anatomy of their stems is unique, the vascular anatomy of their leaves truly cycadean, their seed attachment clearly Stachyospermes and their stomatal structure fundamentally Bennettitales.

Besides the Rajmahal Hills there is in India another basaltic area located in the Central Provinces, the well known Deccan Plateau, famous for the beautiful preservation of the plants embedded in the Deccan Intertrappean cherts (Early tertiary). A material consisting of stems, leaf-sheaths and roots of a palm is described in the paper of Professor B. Sahni and K. R. Surange.[5] Curiously enough, the fossil palm shares, to a certain extent, characters found in the related South American family *Cyclanthaceae* of which no fossil record is so far known. An unusual clumped habit is shown by a specimen that has revealed a main rhizome-like stem producing a pair of large buds which developed into new rhizomes, growing right and left of the main stem. The junior author considers these specimens as representative members of a palm which nevertheless is unlike any of the palms so far known, but show some resemblance with Cyclanthaceae. Among other features the compound nature of the bundle in the central part of the fossil stems is

[3] Bose, M. N., *Bucklandia Sahnii* sp. nov. from the jurassic of the Rajmahal Hills, Bihar. Pp. 41–49.

[4] Vishnu-Mittre, A male flower of the Pentoxyleae stem with stem with remarks on the structure of the female cones of the group. Pp. 75–84.

[5] Sahni, B., and K. R. Surange, On the structure and affinities of *Cyclanthodendron Sahnii* (Rode) Sahni and Surange from the Deccan Intertrappean series. Pp. 93–100.

considered as the most important evidence in favor of affinity with the Cyclanthaceae.

At present our knowledge of the Lower Gondwana plants comes mainly from impressions of the megaflora among which, however, fructifications are poorly represented. Therefore, it is interesting to see that megaspore analysis of two coal seams promises rich results as stated by the researches of K. R. Surange and P. N. Srivastava.[6] The Indian Lower Gondwana coal is usually considered to be formed from the Glossopteris flora which is poor in Lycopod records except *Bothrodendron* sp. Nevertheless, some Indian coal seams are exceptionally rich in megaspores. Nearly all of these show the characteristics of the genus *Triletes* Reinsch, as emended by Schopf which, generally, is considered of probable lycopod affinity. Thus it appears that lycopods must have existed in India despite the scarcity of their impressions. An interesting fact is that, before the extensive glaciation that occurred at the end of the Carboniferous period in the southern hemisphere, lycopod impressions were recorded in countries of Gondwana. It is significant that some of them at least were different from those found in the northern hemisphere, likewise some of the megaspores are distinct from the species of Europe and North America. "This strengthens Sahni's suggestion that the Lycopod of the Glossopteris floras evolved from pre-Gondwana Lycopodes of the southern hemisphere."

One step is made in our knowledge of *Walkomiella Indica*, a primitive conifer of uncertain systematic position: conifer or taxad created for leaf impressions found in the Pindra seam Lower Gondwana, and described by K. R. Surange and Prem Singh. Bulk macerations of coal of the same seam, made by the authors,[7] have yielded seeds still attached to small shoots the epidermal characters of which are identical with those of *Walkomiella Indica* leaves. Accordingly the authors are inclined to assign that female dwarf shoot to *W. Indica*. They also consider that there are indications that the plant bore loosely constructed cones of essentially the same type as in *Lebachia*.

[6] Surange, K. R., and P. N. Srivastava, Megaspore from the West Bokaro coalfield (Lower Gondwana) of Bihar. Pp. 9–17.

[7] Surange, K. R., and Singh Prem, The female dwarf shoot of *Walkomiella Indica*, a conifer from the Lower Gondwana of India. Pp. 5–8.

One short paper, left unfinished by the late Professor Birbal Sahni,[8] and completed by Professor T. M. Harris, F.R.S. of the University of Reading, England, deals with some psilophyte remains found in Silurian or Ordovician strata of Spiti, North-West Himalaya. Despite the poor state of preservation of the material, the potential importance of it is great, for it extends considerably the geographic dispersion of the Psilophytes. This widespread group of plants was known to occur in Silurian up to middle Devonian and in Canada, U. S. A., Europe and China. Were the poor allochtonous relics of Spiti increased in quantity and quality, they would focus attention on a fossiliferous geological horizon from which important revelations are to be expected.

Volume 12 of "The Paleobotanist" demonstrates that excellent results have been obtained by a keen team of workers and, at the same time, it affords undeniable evidence of the great and varied possibilities of Indian sedimentary rocks for palaeobotanical researches. It is significant that the whole material described has been collected in various provinces of India. While the Rajmahal Hills of Bihar and the cherts of the Deccan Intertrappean Series of the Central Provinces are favorite hunting ground for Indian palaeobotanists, the Gondwana formations represent another famous fossiliferous field. A good deal of attention has also been concentrated on Tertiary exposures located in South India in the vicinity of Pondichery, and increasing application in explorations is devoted to fossiliferous deposits of different geological ages of Kashmir, and of the foot hill of the Himalayas. Microfossil investigations of fossiliferous and apparently barren sediments have given excellent results, and have proved their usefulness for scientific and economic purposes.

Every reader interested in the past history of plants, their peculiar morphology and habit, and who is conscious of the important message that palaeobotany offers in regard to the evolution of the plant kingdom and of problems connected with it, should find in volume 12 of "The Palaeobotanist" a good deal of matter for thought.

Much of this volume has received the devoted help of Professor O. A. Hoeg, Professor of Oslo University, Norway, and, at that time, Director of the Birbal Sahni Institute of Palaeontology, Lucknow.

[8] Sahni, B., Note on some possible Psilophytic remains from Spiti, North-West Himalaya. Pp. 1–3.

# GENETIC ASSIMILATION: ADAPTATION VERSUS ADAPTABILITY

FREDERICK E. WARBURTON

*Prince Edward Island Biological Station, Ellerslie, P.E.I., Canada*

In a series of papers, (1942, 1952, 1953a, 1953b) C. H. Waddington has advanced a hypothesis of "genetic assimilation of acquired characters" briefly outlined in a more recent (1956) paper: "Some years ago it was suggested that if selection was practiced for the readiness of a strain of organisms to respond to an environmental stimulus in a particular manner, genotypes might eventually be produced which would develop into the favored phenotype even in the absence of the environmental stimulus." This hypothesis is clearly neither Lamarckian nor Lysenkoist, and is distinct from the "stabilizing selection" of Kirpichnokov (1947) and Schmalhausen (1949), which has been ably and deservedly criticized by Waddington (1953c). Two published experiments (Waddington, 1952, 1953a, 1956) supply strong support for the idea that genetic assimilation may be a powerful evolutionary force in populations of Drosophila.

However, Waddington himself has not lacked critics. To one of these (Underwood, 1954), he replies (1956) "Another point raised by Underwood is . . . that if a genotype can respond adaptively to the environment it normally meets, genetic assimilation of the adaptive phenotypic characters will be unnecessary. On *a priori* grounds, the argument may seem plausible but the fact is that most adaptive features of animals are genetically fixed, and do not alter much when development takes place in somewhat unusual conditions. It is not entirely clear why this should be so; possibly because it is difficult to build up a genotype which develops with the right degree of adaptive modification to the whole range of environments it has to meet, and that it 'pays better' to sacrifice something of the flexibility of the developmental system and to assimilate genetically the adaptation to the most usual environment."

It is easy to array a mass of facts against this unsupported generalization. For example, we need no formal references to prove that in mammals the sizes of the heart and skeletal muscles (surely "adaptive features") are genetically determined only within very broad limits, and vary exquisitely with the demands of the environment. In frog tadpoles, gut length adapts itself to diet (Babák, 1903). In man, if a blood vessel is destroyed by the vicissitudes of the environment, collateral vessels soon increase in size to replace its function; indeed, in the chick embryo, ligation of the right aortic arches leads to establishment of the left, normally lost, as the main artery of the body (Barth, 1953). The haemoglobin concentration of mammalian blood, far from being genetically fixed, varies adaptively with altitude (Haldane, 1917, 1922). The trabeculae of mammalian bones form a pattern beautifully adapted to the stresses they must resist, form different but equally adaptive patterns if the stresses are abnormal, and form no recognizable pattern at all if they carry no load (Murray, 1936; Thompson, 1942). Much of the writer's last paper (Warburton, 1955) strove to show that the size of the mammalian kidney is not fixed, but adapts itself readily to changes in diet or injury to its partner.

Bidder (1923) has shown that the oscula of sponges tend to be so placed that the exhaled water is propelled as far as possible away from the incurrent openings; he suggests that fan-shaped sponges with oscula only on the down-current side grow in areas in which the current is always in the same direction, but if the current turns tidally from all points of the compass, the same type of sponge becomes goblet-shaped, with the oscula opening upward. Kitching (1938) reviews examples of marine and parasitic protozoa which lack contractile vacuoles in their normal environments, but develop them when transferred to hypotonic solutions. Oliver (1894) discusses several plants which produce smooth green leaves in shaded places, but develop protective violet pigments or become "shrouded in thick gray or white fur" in brilliant sunshine; the leaves of Irises, compass plants, etc., are vertical in their normal open habitats, but if seeds of such plants germinate in shady woods the leaves grow horizontally or twist themselves into unusual positions to attain maximum illumination.

These are all cases in which, apparently, it has not "paid better" to sacrifice developmental flexibility, but in which a genotype has evolved which can develop "with the right degree of adaptive modification to the whole range of environments it has to meet." They illustrate the "feedback" type of environmental modification, in which an environmental stimulus causes a morphological change which adapts the organism specifically to that stimulus. Decreased air pressure is followed by adaptation of the blood to decreased air pressure; a change in weight distribution is followed by adaptation of bones to the new weight distribution. In other words, if the environment disturbs the function

of an organ, the organ may be modified until it again functions properly.

Waddington's two experiments, however, involve a fundamentally different sort of adaptation, in which an environmental stimulus (heat treatment of pupae, or etherization of eggs) causes a morphological change (crossveinlessness, bithorax) which does not adapt the organism to the stimulus producing it but to a quite unrelated environmental factor (in this case, the experimenter's selection; i.e., a peculiar form of predation). In such non-feedback adaptation, the modification may well be selectively advantageous in the absence of the environmental stimulus usually causing it, and may tend to be genetically assimilated. Equally obviously, a feedback adaptation is without advantage in the absence of the stimulus causing it, and there will be no selection tending to assimilate it. If heat treatment renders an organism less susceptible to predation, then the same change will be advantageous if it occurs without the heat treatment; but if heat treatment renders the organism less susceptible to heat, the same change will have no advantage whatever in the absence of heat stimuli.

Feedback adaptations may occur in insects. The bug *Rhodnius*, for example, feeds once per instar; the extent of folding in the new cuticle laid down in prepartion for moulting varies with the size of the meal, adapting itself to the amount of growth which will be made. In many insects the corpus allatum of the brain secretes a hormone involved in yolk deposition in the eggs; the enlargement of the corpus allatum observed after removal of the ovaries could be interpreted as compensatory hypertrophy (Wigglesworth, 1954). Worker bees each act as nurses, wax producers and foragers in that order during their imaginal lives; if all young workers are removed from a hive, foragers may redevelop their wax-glands or "nurse-glands" and return to behaviour characteristic of their earlier lives (von Frisch, 1954).

Feedback adaptation is uncommon in insects, however, because of a fundamental characteristic of their development. Unlike the viscera, skin and bones of vertebrates, and the leaves, roots and stems of plants, the exoskeletal structures of an insect (which are those chiefly studied) are quite unable to function while they are still capable of structural change, and cannot change adaptively once they have begun to function. Unlike the muscles or kidneys of a mammal, the wing of an insect cannot increase in size through increased use, since it cannot be used at all until it has become hardened and rigid and incapable of structural change.

The evolution of adaptations has been the subject of genetic research and speculation for decades; study of the evolution of adaptability has been hampered by several things. A fundamental one, now fortunately disappearing with the rise of modern developmental and physiological genetics, is the idea that genes determine static anatomical "characters," rather than that they influence processes. Another is the common tendency to discontinue embroyological experiments in the early stages of development, often before many organs have begun to function, and to confine studies of environmental effects in development to "shock treatment" experiments (such as exposing pregnant mice to one brief but severe period of anoxia, or injecting massive single doses of insulin into developing eggs), rather than to observe the effects of persistent small environmental changes (such as slight but continued hypoxia or hyperinsulinism). A third is the application of conclusions from experiments on arthropods, such as Drosophila, in which adaptability is known to be greatly restricted by the nature of development, to other organisms in which no such restriction exists.

Since genotypes are inherited but phenotypes are selected, the evolutionist must concern himself with the interaction of heredity and environment in the development of the individual. However, he must not have his hypotheses restricted by the developmental limitations of a single phylum, but must recognize and study the different modes of interaction available to different groups of organisms. Perhaps not all of these modes are exemplified by Drosophila.

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## CLIMATIC RULES

P. F. SCHOLANDER

*Institute of Zoophysiology, University of Oslo*

In reply to the interesting comments by Newman and Mayr (EVOLUTION 1956) on my article "Evolution of Climatic Adaptation in Homeotherms" (EVOLUTION 1955) I shall restate the issue I raised, namely: What is the evidence that the slight biometrical trends expressed in Bergmann's and Allen's rules represent a physiological adaptation to temperature?

Clearly, the first prerequisite must be to establish that the observed size cline is associated with a falling environmental temperature going north. Among Eskimos, Lapps and other northern people the thermal environment which is most relevant to our problem exists inside the clothing, and so far this has not been measured. The indications are that it is as tropical as ours. The argument that Eskimos frequently suffer loss of toes from frostbite seems to be controversial; it was termed utter nonsense by a physician stationed among the Thule Eskimos in North Greenland, and statements to the same effect were made to me by people who have intimate knowledge of the Lapps and Chukchees. Whether, as Newman suggests, the primeval Eskimos went through "long-term experimentation" and considerable freezing before they learned to make clothing is something else again.

I pointed out that the biometrical clines expressed in Bergmann's and Allen's rules are based on measurements which are irrelevant or at best uninterpretable as a means for appraising the thermal adjustment of the animal. Whether or not the subspecific, generally minute and erratic size trends have anything to do with heat conservation and thermo adaptation cannot therefore be determined from such data. But the whole thesis is badly shaken, not to say demolished, by the flagrant lack of general validity of the rules which is apparent when we look for similar trends on a species level. Here neither the biometry of the rules nor their fancied physiological interpretation hold. It should also sound a warning that similar size clines are found in many cold-blooded animals where thermal implications clearly are out of the question.

Mayr, banking on geometry and logics, nevertheless considers the thermo adaptive implications of the rules so firmly established that the emphasis of research should rather be shifted to an analysis of the exceptions. As an example of such an analysis, i.e., of an exception to an unproven thesis, is cited among others the case of the titmouse (Snow, EVOLUTION 1954). In several species of European titmice the length of the beak, divided by that of the wing feathers, decreases going northward. This, of course, harmonizes with Allen's rule, and is construed as a straightforward effect of cold on the beak. In two species, however, it is remarkable that beyond a certain northern limit the bill shrinks no farther. Since every exception to the ecogeographical rules is considered to be an indication of a selection conflict, what is the conflicting selection pressure that has checked the shrinking of the titmouse's bill? Clearly if the cold had shrunk the beak away, eating would be difficult, and so the conflicting pressure must lie in the eating process.

This inference is indeed supported by unpublished quantitative observations to the effect that not only the size of food particles but also the amount taken by these birds is such that eating would be seriously hampered if the bill should shrink any more. I take it that the result of these fanciful constructions must be a scrawny titmouse striving to attain a size to fit the climate, but frustrated by a cold beak not much good to eat with.

The titmouse shows another equally remarkable deviation from Allen's rule: Its tail feathers, oblivious to the cold, grow longer going north. This must also be an adaptation, according to Mayr, because "a close parallelism between character gradients and environmental gradients, if found to have a genetic basis, is interpreted with good reason as being the result of natural selection." One may well ask: Selection of a long tail for what? I shall abstain from joining a free-for-all on the question of how the titmouse got its tail.

Mayr suggests that exceptions to the rules in other groups of animals should be analyzed in a similar way, so let us consider the American otter. This animal defies Bergmann's rule by getting smaller going north. What is the selection pressure that shrank the northern otter? I would like to suggest that the conflicting pressure may be traced to the squeeze of the ice-hole. Whenever the ice-hole tends to freeze shut in the winter the otter cannot pass through it without being subjected to a certain degree of "selection squeeze," and the fact that today this pressure may be so slight as to be unmeasurable serves only to prove the great delicacy of the selection process, or if this argument is not adequate we need only invoke the Pleistocene, when the otters must certainly have undergone a "long-term experimentation" and considerable squeezing while they were learning how to make proper holes. Now, according to Mayr, "it is axiomatic in scientific methodolgy that a hypothesis is considered valid until it has either been disproven or until a better one has been proposed." So I take it this hypothesis must for the present be respected.

It is unnecessary to point out my admiration in general for the great modern synthesis which the science of evolution represents, but I may venture to observe that some examples of adaptive mechanisms are being paraded where the physiological interpretations are taken much too lightly. I appreciate very much that I have been given the opportunity to enter the lions' den and confront morphologically oriented evolutionists with some physiological aspects of a subject of interest to both.

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## CORRECTION

Pollen Dimorphism in the Rubiaceae, H. G. Baker, EVOLUTION, Volume X, Number 1, March 1956, figure 2, p. 26. The letter references A and B are reversed in the figure. 2A should read *Faramea salicifolia* (not *F. occidentalis*) and 2B should read Faramea occidentalis (not *F. salicifolia*). Also the scale was omitted. Magnification is × 273.